MYSIS DILUVIANA IN THE GREAT LAKES: HISTORIC DRIVERS OF ABUNDANCE AND PRODUCTION, AND CURRENT STATUS IN LAKE ONTARIO

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ABSTRACT

Mysis diluviana are small, shrimp-like crustaceans native to the Laurentian Great Lakes, where they are important as planktivores and as prey for fish. Therefore, our understanding of offshore Great Lakes food webs requires an understanding of *M. diluviana* population dynamics in these systems. In this thesis, I review the factors observed to influence the abundance, life history, and production of *M. diluviana* in the Great Lakes, and report recent status (2013) in Lake Ontario, including the first production estimate since 1995. In Lake Ontario in 2013, *M. diluviana* abundance, biomass, and production were less than 50% of values in the 1990s, but age-0 growth rate and age-1 fecundity were higher. These results suggest food limitation was not the cause of the observed declines in abundance in the late 1990s.

BIOGRAPHICAL SKETCH

Toby Holda was born in Chicago, Illinois where took a special interest in fish, fishing, aquatic organisms, and science before graduating high school in 2009. He then attended the College of DuPage until 2011, when he transferred to the University of Illinois at Urbana-Champaign. There, he was an active member of the university American Fisheries Society (AFS) subunit, and participated in undergrad research in the Cáceres and Wahl labs. He completed the degree for Bachelor of Science in Natural Resources and Environmental Sciences in the spring of 2013. In the summer of 2013, Toby began working as a graduate student for professor Lars Rudstam of the Cornell Biological Field Station in the Department of Natural Resources at Cornell University, where he has studied fisheries acoustics and mysid shrimp biology. In his time as a graduate student, Toby has been an active member of the AFS subunit at Cornell University. He also enjoys listening to books, running, skiing (cross-country), strategy games, relaxed sports, and spending time with friends.

To my Family

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CHAPTER 1

FACTORS AFFECTING THE ABUNDANCE, LIFE HISTORY, AND PRODUCTION OF *MYSIS DILUVIANA* IN THE LAURENTIAN GREAT LAKES: A REVIEW

Abstract

Mysis diluviana are small, shrimp-like crustaceans native to deep lakes in North America. They are abundant in offshore regions of four of the five Great Lakes (Superior, Michigan, Huron, and Ontario), where they are important as planktivores and as prey for fish. Therefore, our understanding of offshore Great Lakes food webs requires an understanding of *M. diluviana* population dynamics in these systems. I reviewed the literature on Great Lakes *M. diluviana* population dynamics, searching for factors observed to influence their abundance, life history, and production. Abiotic factors considered important in the literature are: 1) basin morphology, which determines thermal regime and thus distribution and metabolic rates of *M. diluviana*; 2) bottom depth, which influences the overlap of *M. diluviana* and their predators; higher overlap in shallow water is believed to result in higher mortality and lower density of *M. diluviana* nearshore; 3) currents and gyres, which can shift *M. diluviana* distributions and may result in greater overlap with predators; and 4) vertical temperature and light profiles, which determine offshore nighttime overlap with predators and prey during the summer stratified period. Biotic factors considered important include: 1) overall system productivity and food resource availability, which influences life history rates and fecundity, and has greater impact on juvenile *M. diluviana* than on adult *M. diluviana*; 2) predation pressure which has greater impact

on adult *M. diluviana* than on juvenile *M. diluviana*; 3) presence or absence of abundant offshore populations of *M. diluviana* predators, which reduce otherwise high offshore abundances of *M. diluviana*; and 4) loss of abundant *Diporeia* populations that, when present, dilute predation pressure on *M. diluviana*.

Introduction

Mysis diluviana (Audzijonyté and Väinölä, 2005; formerly *Mysis relicta* Lovén) are freshwater members of the Mysidaceae (Crustacea). Mysids are collectively called, "opossum shrimp," due to the presence of a brood pouch in gravid females for carrying developing embryos. *M. diluviana* is one of five species in the *M. relicta* complex, a group of brackish and fresh water glacial relict species with a collectively circumpolar distribution (Audzijonyté and Väinölä, 2005). *M. diluviana* reach up to 25-30 mm in length (Mauchline, 1980; Rudstam, 2009), and are native to North America. They are found in all five Laurentian Great Lakes, in the New York Finger Lakes, in Lake Champlain, and in several smaller lakes in Canada and the northern United States of America.

While *M. diluviana* are present in all five Great Lakes, they are only abundant in four (Superior, Michigan, Huron, and Ontario), where they are important members of offshore food webs. Abundances in Lake Huron are lower than the other three lakes in this group (Jude et al., *in preparation*). In contrast, while *M. diluviana* have been detected in Lake Erie, these detections have been limited to the eastern basin and densities have always been low (when detected = 0.3 – 2.5 /m^2) (Carpenter et al., 1974; Jude et al., *in preparation*). Seasonal lake-wide and offshore densities in the other four lakes typically range from 40 - 200 /m^2, while highest recorded catches in individual net hauls have exceeded 1000 /m^2 (Carpenter et al, 1974; Johannsson et al., 2003; Pothoven et al., 2010; Watkins et al., 2015). The highest densities of *M. diluviana* observed in the Great Lakes were from Lake Ontario (Carpenter et al., 1974; Johannsson et al., 2003; Jude et al., *in preparation*), where *M. diluviana* have been

found to make up 10-30% of the pelagic crustacean zooplankton (Watkins et al., 2015; *Chapter 2*).

M. diluviana are important both as predators and prey. Since they are so abundant, the *M. diluviana* population can consume more zooplankton than fish planktivores in offshore areas (Johannsson et al., 1994; Gal et al., 2006; Bunnell et al., 2011). *M. diluviana* in the Great Lakes also feed on phytoplankton, especially in the spring when zooplankton are less abundant (Bowers and Grossnickle, 1978; Grossnickle, 1982; O'Malley and Bunnell, 2014; O'Malley et al., 2017). As prey, *M. diluviana* can make up a high proportion of the diet by biomass of several fish species in the Great Lakes. Specific examples include: yellow perch (*Perca flavescens*, 90% *M. diluviana* in diet), bloater (*Coregonus hoyi*, 30%), and alewife (*Alosa pseudoharengus*, 10%) in Lake Michigan (Wells, 1980; Rand et al., 1995); kiyi (*Coregonus kiyi*, 95%), bloater (95%), smelt (*Osmerus mordax*, 80%), cisco (*Coregonus artedii*, 40%), spoonhead sculpin (*Myoxocephalus thompsonii*, 40%), and siscowet lake trout (*Salvelinus namaycush siscowet*, 20%) in Lake Superior (Gamble et al., 2011); and alewife (60-90%) in Lake Ontario (Walsh et al., 2008; Stewart et al., 2009). These observations indicate that *M. diluviana* is a key species for the transfer of energy up the trophic levels of the food web from plankton to fish. This conclusion is corroborated by food web models (Stewart and Sprules, 2011).

Thus, our understanding of Great Lakes food webs is greatly informed by our understanding of the status and drivers of *M. diluviana* population dynamics in the Great Lakes. For this literature review, I was interested in exploring patterns in the influence of abiotic and biotic factors on *M. diluviana* population dynamics. While

this has been examined and discussed for specific lakes, no study has examined this suite of patterns at the multi-lake scale. I reviewed the literature on Great Lakes *M. diluviana* population dynamics, searching for abiotic and biotic factors observed to influence *M. diluviana* abundance, life history, and production in the Great Lakes.

Abiotic Factors

Here, I seek to demonstrate that the following observations are substantiated in the literature. These include that: 1) basin morphology and resulting thermal regimes limit *M. diluviana* distribution and affect life history rates (thermal regime here defined as the seasonal pattern of vertically-distributed thermal conditions in the lake environment); 2) bottom depth is the most important predictor of *M. diluviana* density across all five Great Lakes, likely due to depth-dependent patterns of spatial overlap between *M. diluviana* and predators; 3) currents, upwelling events, and the mixing effect of winter storms all redistribute *M. diluviana*, placing some *M. diluviana* in shallower areas nearshore where they are more vulnerable to predation risk; and 4) in the summer stratified period in offshore areas, vertical temperature and light profiles determine spatial overlap of *M. diluviana* with their predators and prey.

Basin Morphology and Thermal Regime

Basin morphology determines thermal regime of dimictic lakes like the Great Lakes (Wetzel, 1975), and thus influences *M. diluviana* population dynamics. There are two main reasons for this. The first is that *M. diluviana* are adapted to live in cold temperatures year-round (Ricker, 1959; Rudstam et al., 1998; Rudstam, 2009).

Specifically, the findings of several field and laboratory studies demonstrate that adult *M. diluviana* typically avoid temperatures above 9-12 °C, can tolerate short-term exposure to temperatures up to 14-16 °C to gain access to food, and are quite intolerant to temperatures above 18-20 °C (Ricker, 1959; Beeton, 1960; Smith, 1970; Beeton and Bowers, 1982; Rudstam et al., 1999; Boscarino et al., 2007). This likely explains the restriction of *M. diluviana* in Lake Erie to only the eastern basin (Carpenter et al., 1974; Jude et al., *in preparation*). Each summer, the western basin typically exceeds 16 °C for four months and 20 °C for two months, and the central basin typically exceeds 12 °C for two months and 16 °C for one month (Schertzer et al., 1987). In the Eastern basin, at least 20 m of water is maintained at ≤ 12 °C most summers, only rarely exceeding 16 °C (Schertzer et al., 1987). It is important to note that the hypolimnion of Lake Erie's central basin experiences annual oxygen depletion (Burns et al., 2005), which likely also prevents *M. diluviana* from establishing in that basin. Most mysid species are limited to environments with relatively high oxygen concentrations, and this includes *M. diluviana* (Mauchline, 1980; Rudstam, 2009).

The second reason thermal regime and thermal structure is important for *M. diluviana* is that they are ectothermic, relying on external thermal conditions to regulate rates of consumption, metabolism, growth, and reproduction (Berill and Lasenby, 1983; Chipps, 1998; Rudstam et al., 1999). An increase in the surrounding temperature of *M. diluviana* from 5 °C to 10 °C can result in higher consumption, growth, and respiration rates, leading to shorter generation times and increased fecundity (Sandeman and Lasenby, 1980; Berrill and Lasenby, 1983; Chipps, 1998; Rudstam et al., 1999). This effect is easily demonstrated in eastern Lake Erie. Only

three gravid *M. diluviana* were collected from eastern Lake Erie during 2006 to 2014; however, they were all ≥ 15 mm and had the highest mean size-adjusted brood size found in any of the Great Lakes (ANCOVA, df = 5, 509, F = 25.9, $p < 0.001$; Holda, *unpubl. data*). This may be due to thermal conditions of eastern Lake Erie, where hypolimnetic temperatures often exceed 9 °C (Schertzer et al., 1987). An alternative explanation for high fecundity in eastern Lake Erie is high lake productivity (see *Biotic Factors* section). Notice that this high fecundity also implies a high mortality given the very low densities observed in Lake Erie.

Bottom Depth

Where *M. diluviana* are present, bottom depth in relation to light and temperature gradients in the water column imposes a spatial structure that influences their overlap with predators and food resources, and thus influences patterns of predation, mortality, abundance, and food availability. *M. diluviana* spend much of their time near the bottom of the lake to avoid predators. Thus, to support *M. diluviana* populations, a lake basin has to be deep enough to allow for a low-light refuge from predators throughout the year (Tattersall and Tattersall, 1959; Rudstam, 2009). Since bottom depth is a feature of the lake environment which spatially organizes many other biotic and abiotic factors important to *M. diluviana* population dynamics, it turns out to be an important predictor of areal density for that species (Johannsson 1992, 1995; Rudstam et al., 2008). *M. diluviana* were rarely found at bottom depths shallower than 50 m (Carpenter et al., 1974; Johannsson 1995; Johannsson et al., 2003; Jude et al., *in preparation*), and their areal density has been observed to increase with depth steadily up to depths of 100m (Johannsson 1995; Pothoven et al., 2004; Rudstam et al., 2008;

Chapter 2). In Lakes Michigan and Superior, *M. diluviana* abundance continues to increase with bottom depth in water deeper than 100 m (McWilliam, 1970; Sierszen et al., 2011; 2014). In Lake Ontario, areal densities in water with bottom depths greater than 100m tend to be more variable and increase only slightly with bottom depth (Johannsson, 1995; Johannsson et al., 2003; Watkins et al., 2015). Johannsson (1995) hypothesized this pattern of increasing areal density with greater bottom depth is due to higher predation pressure from nearshore alewives during the fall-spring (see Bergsted and O'Gorman, 1989; Mills et al., 1992; Stewart et al., 2009). In Lake Michigan, density and production of *M. diluviana* increased with depth offshore despite higher system productivity nearshore (Lehman et al., 1990; Pothoven et al., 2000; 2004; Sell, 1982). As in Lake Ontario, Pothoven et al. (2000) and Lehman et al. (1990) suggested this was due to greater predation pressure nearshore where planktivore densities were higher (Brandt et al., 1991).

These bottom-depth driven patterns in densities of *M. diluviana* may result in higher growth nearshore than offshore (i.e., reduced resource competition nearshore). Johannsson et al. (1994) found that bioenergetically-modeled consumption demands of *M. diluviana* increased with bottom depth in both Lakes Michigan and Ontario, although this happened at shallower depths in Lake Ontario than in Lake Michigan. In Lake Ontario, Johannsson et al. (1994) found that modeled consumption demand of *M. diluviana* was less than 20% of zooplankton production at depths <100m, but over 100% of zooplankton production at depth >200m. Johannsson et al. (1994) did not evaluate proportional demand in Lake Michigan due to insufficient information on zooplankton production. Several studies have found that growth rates in Lake

Michigan were higher nearshore than offshore (Beeton and Gannon, 1991; Reynolds and DeGrave, 1972). This supports the idea that resource competition may be greater offshore due to higher densities of *M. diluviana*. In further support of this idea, reductions in lake-wide productivity which were more pronounced in the nearshore (Fahnenstiel et al., 1998) may have resulted in the observed decline of nearshore *M. diluviana* growth rates to similar levels as offshore growth rates (Pothoven et al., 2000).

Currents, Upwelling Events, and Winter Storms

Currents, upwelling events, and winter storms are another set of abiotic factors suspected to influence *M. diluviana* horizontal distributions and thus ultimately productivity. While horizontal patterns in *M. diluviana* densities are highly correlated with bottom depth at the lake-wide scale, they are often spatially patchy on smaller scales (< 1 km) (Pothoven et al., 2004; Watkins et al., 2015). Currents have been suggested as potential explanations of horizontal patchiness and mid-lake "holes" in offshore *M. diluviana* densities (Rudstam et al., 2008; Watkins et al., 2015). Upwelling events have been proposed as explanations for observed horizontal migrations of *M. diluviana* in Lakes Michigan and Ontario (Shea and Makarewicz, 1989; Johannsson, 1992; 1995). Winter storms and currents have been suggested as an explanation for more uniform spring distributions (Reynolds and DeGraeve, 1972; Johannsson, 1995). All of these processes directly alter local densities. However, they may also shift more *M. diluviana* nearshore, in spatial overlap with predators, thereby increasing overall mortality at the lake-wide scale. This may also set up the summer and fall bottom-depth related density patterns.

Offshore Light and Temperature Profiles

In offshore stratified waters during the summer, night time light profiles (produced by moonlight, starlight, and sometimes by coastal city lights) and temperature profiles determine night time foraging success and predation risk of *M. diluviana* in the metalimnion and upper hypolimnion. *M. diluviana* perform diel vertical migration, avoiding visual predators by day in the dark hypolimnetic waters, and rising under cover of night to the lower metalimnion to feed on plankton (Beeton, 1960; Gal et al., 2004). The exact depth and vertical extent of *M. diluviana* nighttime vertical distributions can be predicted from ambient light and temperature profiles in the lake (Boscarino et al., 2009; 2010b). The resulting overlap of these distributions mediates the degree of predator-prey interactions involving *M. diluviana*. Boscarino et al. (2010b) predicted that when penetration of the water column at night by ambient light is deep relative to the thermocline – such as under a full moon or in clearer water – *M. diluviana* will be deeper in the water column and have less spatial overlap with predators; however, they also predicted that overall mortality of *M. diluviana* will be higher on such nights since predators were found to be much better at capturing *M. diluviana* at these light levels.

Biotic Factors

I grouped the biotic factors observed to influence *M. diluviana* population dynamics in the Great Lakes into effects caused by food resource availability, which includes any impact of resource competition, predation pressure, and community

composition. As I hope to demonstrate in the following paragraphs, evidence from the literature suggests that: 1) lake trophic state is generally correlated with *Mysis spp.* life history rates; 2) correlation between food resource availability and abundance and possibly growth rate tended to be stronger for juvenile *M. diluviana* than for adult *M. diluviana*; 3) predation pressure was often more strongly correlated with abundance and overwinter survival of adult *M. diluviana* than of juvenile *M. diluviana*; 4) abundant deep water *M. diluviana* predator species in a lake may reduce the strength of the correlation between bottom depth and *M. diluviana* densities; and 5) loss of *Diporeia* may remove a buffer to deep water predation pressure on *M. diluviana*, resulting in reduced offshore densities.

Lake Trophic State

Lake trophic state is an overall measure of how biologically productive (i.e., how, "green") a lake is (usually expressed in terms of spring total phosphorous concentrations). Lake trophic state has been broadly related to overall life history rates of *Mysis spp.* in the Great Lakes and elsewhere (Beeton and Gannon, 1991; Penk et al., 2016). This pattern is noticeable in the comparison of Lake Michigan to the rest of the Great Lakes during the 1970s. Lake Michigan was more productive during that time (Barbiero et al., 2012; 2015). At the same time Lake Michigan had the shortest *M. diluviana* generation time (embryo to first reproduction; 1.5 years) of the Great Lakes, and these organisms may have regularly participated in two reproductive pulses per lifecycle (Reynolds and DeGraeve, 1972; Morgan and Beeton, 1978). The effect of trophic state can also be seen in Lake Ontario, which continues to have the highest spring total phosphorous concentrations of the four deep Great Lakes (Bunnell et al.,

2014a; Barbiero et al., 2015). Throughout the 2000's, *M. diluviana* in Lake Ontario had the fastest mean growth rate and highest mean size-at-age observed in the Great Lakes (Jude et al., *in preparation*).

Food Resource Availability

Within *M. diluviana* populations, food resource availability has been related to reproductive effort. Johannsson et al. (2011) observed a significant positive relationship between a fall zooplankton biomass index and the size-adjusted fecundity of gravid females in this time period. Beeton and Gannon (1991) report declining generation time and increasing growth rate and fecundity of *M. relicta* (Lovén; some *M. relicta*, some *M. diluviana*) with increasing lake-wide production in a review of 11 lakes across Europe and North America. In contrast, I observed increased age-0 growth and age-1 fecundity of *M. diluviana* in Lake Ontario in 2013 relative to Lake Ontario in 1990 when production of zooplankton and phytoplankton was higher than in the 2000s (Rudstam et al., *in press*; Scofield et al., 2017, *Chapter 2*). I believe this is the result of 1) lower density and increased mortality of *M. diluviana* in 2013 and 2) a shift in the distribution of food resources to deeper layers where *M. diluviana* feed. Those two trends could work together to reduce the consumption demands of the *M. diluviana* population relative to the food production available to it.

Food resource availability was also more commonly correlated with population dynamics of juvenile *M. diluviana* than of adult *M. diluviana*. Pothoven et al. (2010) observed a positive correlation between spring whole water column chlorophyll-a concentrations and *M. diluviana* new recruit abundance from 1995 – 2008, based on

surveys of a nearshore-offshore transect in southern Lake Michigan. *M. diluviana* new recruit abundance was not correlated with summer-fall chlorophyll-a concentrations, suggesting juvenile *M. diluviana* may be limited by the spring phytoplankton bloom. If true, years with low spring chlorophyll-a concentrations ought to be accompanied by reduced age-0 growth. However, Pothoven et al. observed no difference in growth between the late 1990s (higher chlorophyll-a) and the late 2000s (lower chlorophyll-a), although any reduction in growth rates might have occurred too early to be observed by their survey. Johannsson et al. (2011) observed strong positive relationships between two zooplankton biomass indices and both the proportion of *M. diluviana* <6 mm long and the abundance of the age-0 cohort in Lake Ontario in the early 2000s. Johannsson et al. also observed a strong negative relationship between juvenile overwinter mortality and zooplankton biomass. In the spring, newly-released *M. diluviana* are more dependent on algal food resources, while older *M. diluviana* rely more on zooplankton as reflected in having a higher proportion of zooplankton in their diets (Grossnickle, 1982; O'Malley et al., 2017). Pothoven et al. (2010) suggest the limitation of juveniles to algae could explain observed age-specific effects of algal concentrations. An alternate explanation is that reproduction is reduced in low food years, resulting in weaker year classes. However, reproductive effort was similar and had not changed over time in the study from Lake Michigan (Pothoven et al., 2010).

Overall Predation Pressure

Variable fish predation was more commonly correlated with mortality of adult *M. diluviana* than of juvenile *M. diluviana*. Johannsson et al. (2011) found strong correlation between predation indices (based on abundance and size-selective

predation of alewife and smelt) and both age-1 over winter mortality (positive correlation) and also age-2 abundance (negative correlation). The correlation with age-0 abundance was not significant.

Offshore Predator Populations

Abundant populations of deepwater *M. diluviana* predators are likely to reduce the protection of *M. diluviana* deepwater refuges. McDonald et al. (1990) suggested that dramatic offshore declines of *M. diluviana* densities from 1980 to 1985 were due to a shift in prey fish biomass from alewife, which are pelagic when offshore, to bloater, which primarily inhabit deep water when offshore. The predator-shift effect was supported by Pothoven et al. (2010), who attributed the recovery of *M. diluviana* by 1995 to declining numbers of bloaters. In Lake Ontario, *M. diluviana* have an effective offshore deepwater refuge, since deepwater *M. diluviana* predators in this lake are all either extirpated (kiyi and bloater) (Zimmerman and Krueger, 2009) or scarce (rainbow smelt *Osmerus mordax*; Walsh et al., 2015; and slimy sculpins; Weidel et al., 2015). Interestingly, although current densities of *M. diluviana* in Lake Ontario are lower than historic levels, they appear stable and in 2006-2016 are the highest in the Great Lakes (Johannsson et al., 2011; Rudstam et al., *in press*; *Chapter 2*; Jude et al., *in preparation*).

There are two trends which might weaken the argument that abundant populations of deepwater *M. diluviana* predators are likely to reduce the protection of *M. diluviana* deepwater refuges. First, Lake Ontario, proposed above as a lake without many deepwater *M. diluviana* predators, is not entirely devoid of important deepwater

predators. Deepwater sculpins (*Myoxocephalus thompsoni*) are increasing in Lake Ontario and currently surpass densities seen in other lakes (Brandt, 1986; Weidel et al., 2015). Even in a lake with *Diporeia* present (Lake Superior), deepwater sculpin diets can be found containing more than 50% *M. diluviana* by weight throughout the year (Gamble et al., 2011). Even at low densities deepwater sculpins can substantially reduce *M. diluviana* abundances. Second, while historic fluctuations in offshore *M. diluviana* abundances in Lake Michigan were likely due to fluctuating levels of bloater predation, the current low densities of *M. diluviana* in Lake Michigan are not likely to be due bloater predation alone. Although densities of *M. diluviana* in Lake Michigan have declined since the late 1990s (Pothoven et al., 2010; Jude et al., *in preparation*), bloater in Lake Michigan have consumed a decreasing proportion of available *M. diluviana* production in the last two decades (Pothoven and Bunnell, 2016). Indeed, an alternate explanation is more compelling. Preliminary results indicating growth rates of *M. diluviana* in Lake Michigan have declined to 0.016 mm/d suggests declines in food availability are responsible for current low numbers in that lake (Holda et al., *unpubl. data*).

Loss of Diporeia

The loss of *Diporeia* can increase predation pressure experienced by *M. diluviana*, because *Diporeia* are an alternative prey for *M. diluviana* predators and have similar energy content to *M. diluviana*. Several studies suggest that planktivorous fish shifted to more *M. diluviana*-heavy diets once *Diporeia* disappeared from Lake Michigan (Pothoven and Bunnell, 2016; Pothoven and Madenjian, 2008; Pothoven and Fahnenstiel, 2014), and Lake Ontario (Owens and Dittman, 2003; Walsh et al., 2008;

Stewart et al., 2009). The effect of *Diporeia* on *M. diluviana* population dynamics is demonstrated in the contrasting density trends in the 2000s in Lakes Michigan (where *Diporeia* were in low numbers) and Superior (where *Diporeia* were abundant in the environment and fish diets) (Gamble et al., 2011). Densities of *M. diluviana* from 2006-2014 were increasing slightly in Lake Superior, and stable or declining slightly in Lake Michigan (Jude et al., *in preparation*). While Lake Ontario has higher densities of *M. diluviana* than Michigan, despite having lost *Diporeia*, the lack of abundant deepwater predators and higher lake productivity probably makes the absence of *Diporeia* less critical in Lake Ontario than in Lake Michigan.

Conclusions

I found several general patterns in the effects of abiotic and biotic factors on *M. diluviana* population dynamics. Thermal regimes (as determined by basin morphology) have direct effects on *M. diluviana* physiology, as temperature regulates metabolic rates and can cause mortality. Other abiotic factors tend to influence growth and mortality of *M. diluviana* indirectly by structuring spatial overlap of *M. diluviana* with their prey and predators. Bottom depth is correlated with *M. diluviana* density, because bottom depth determines spatial patterns of other important factors of *M. diluviana* population dynamics, including distributions of predators and primary productivity. Currents, upwelling events, and winter storms redistribute *M. diluviana*, and can move *M. diluviana* to areas of higher predation risk. At night, vertical light and temperature profiles determine offshore spatial overlap of *M. diluviana* with prey

and predators. Some biotic influences demonstrate even stronger effects on particular age-classes of the *M. diluviana* population. Lake trophic state is correlated with life history rates of *Mysis spp*. Food limitation appears to have a greater impact on fecundity and on age-0 animals, while predation appears to have a greater impact on age-1+ animals. Other biotic factors represent the effect of particular species which overlap with *M. diluviana* in the deep offshore zones. Abundant populations of deepwater *M. diluviana* predators may reduce the typically higher abundances of *M. diluviana* observed offshore. *Diporeia*, in contrast, act as an alternate prey source relative to *M. diluviana* and may thus can dilute offshore predation pressure.

CHAPTER 2

LAKE-WIDE SEASONAL GROWTH, REPRODUCTION, DENSITY, AND PRODUCTION OF *MYSIS DILUVIANA* IN LAKE ONTARIO IN 2013

Abstract

Mysis diluviana is a major component of prey fish diets in the Great Lakes making annual production of *M. diluviana* an important metric for understanding and modeling energy flow through Great Lakes food webs. However, there are only three whole lake measurements of annual *M. diluviana* production in Lake Ontario available to date (1971, 1990, and 1995). During 2013, lake-wide coverage of Lake Ontario was achieved for four sampling periods from April – November. Generation time was two years from embryo to first reproduction for most *M. diluviana*. Reproduction took place primarily in early fall. April-November growth rates were 0.052 mm/d for the age-0 cohort and 0.026 mm/d for the age-1 cohort (significantly higher than observed in the 1980s-90s for age-0 - 0.035 mm/d). Annual mean density and biomass of *Mysis* in 2013 were about 60% and 40% of values in the 1990s at 99 /m^2 (SE: 11) and 319 mg dw/m^2 (SE: 28). *Mysis* composed >10% of the offshore crustacean zooplankton biomass in Spring and Summer. Annual production was about 35% of values in the 1990s at 0.85 g dw/m^2/yr (SE: 0.03). Annual production to biomass ratio (P/B) was about 15% lower than in the 1990s, at 2.65 /yr.

Introduction

Mysis diluviana (Audzijonyté and Väinölä, 2005; formerly *Mysis relicta* Lovén) is an important species in the offshore food webs of the Laurentian Great Lakes. In Lake Ontario, *M. diluviana* can reach densities of over 500 /m^2 and can contribute up to a third of the total crustacean zooplankton biomass (Watkins et al., 2015). *M. diluviana* is also an important predator of zooplankton throughout the Great Lakes (Gal et al., 2006; Stewart and Sprules, 2011; O'Malley and Bunnell, 2014; O'Malley et al., 2017), and in offshore areas of Lake Ontario, zooplanktivory by *M. diluviana* can exceed zooplanktivory by fish (Gal et al., 2006). *M. diluviana* is also an important prey species making up 60-90% of Lake Ontario alewife (*Alosa pseudoharengus*) diets by biomass during fall, winter, and spring (Stewart et al., 2009). Alewife, in turn make up 95% of Lake Ontario's pelagic fish biomass and 96% of Lake Ontario Chinook (*Oncorhynchus tshawytscha*) diets by biomass (Stewart and Sprules, 2011; Happel et al., *in press*). In addition, since deep water coregonids depend on *M. diluviana* as prey in other lakes (Gamble et al., 2011; Sierszen et al., 2014), restoring deep water coregonids in Lake Ontario (as advocated by the Great Lakes Fisheries Commission, Zimmerman and Krueger, 2009) is likely to be dependent on *M. diluviana* production.

However, since calculating *M. diluviana* production requires high sampling effort, it has not been estimated for nearly two decades. Reliable *M. diluviana* production estimates require several observations of growth and mortality over a year (Iverson and Dall, 1989; Johannsson, 1992). While there are estimates of *M. diluviana* production in Lake Ontario based on seasonal growth and mortality data throughout the 1980s and 1990s, the most recent estimate is from 1995 (Johannsson et a., 2003).

Further, since *M. diluviana* spatial distribution can change over the season, it is important to conduct lake-wide surveys to avoid confounding migration and mortality. Only three such lake-wide estimates of production have been conducted (1971, 1990, and 1995; Carpenter et al., 1974; Johannsson, 1995; Johannsson et al., 2011). All subsequent estimates have been based on the production-to-biomass ratio (P/B) from 1995 and whole lake fall biomass samples (Johannsson et al., 2011).

Production estimates assuming constant P/B may be sufficient, but there are two reasons why P/B may have changed since 1995. First, there have been several changes in Lake Ontario since the 1990s that could have impacted growth and mortality of *M. diluviana*, such as increases in water clarity (Boscarino et al., 2010; Rudstam et al., *in press*), declines in epilimnetic zooplankton density (Rudstam et al., *in press*), invasions of predatory cladocerans (*Bythotrephes longimanus* and *Cercopagis pengoi*; Johannsson et al., 2011*)* and round goby (*Neogobius melanostomus*; Walsh et al., 2007), an increasing population of deepwater sculpin (*Myxocephalus thompsoni*) (Weidel et al., 2017), and shifts in vertebrate planktivore diets in response to the disappearance of *Diporeia* (Owens and Dittman, 2003; Stewart et al., 2009). All these factors can affect *M. diluviana* growth and mortality rates and therefore production. Second, *M. diluviana* abundance and biomass in Lake Ontario in the 2000s declined by 50% since the 1990s (Johannsson et al., 2011; Rudstam et al., *in press*), which could increase P/B if growth is density dependent. Indeed, this was predicted by Stewart and Sprules (2011). If *M. diluviana* P/B has changed, estimates of current production based on the 1990 or 1995 P/B will be in error.

Given the importance of *M. diluviana* in the Lake Ontario food web (Gal et al., 2006; Stewart and Sprules, 2011), the rarity of annual production estimates for *M. diluviana*, and the possibility of change in P/B, it is important to obtain current estimates of *M. diluviana* production. The Cooperative Science and Monitoring Initiative (CSMI) in 2013 allowed us to conduct the first whole lake, multi seasonal survey of the *M. diluviana* population in Lake Ontario since the 1990s. I was specifically interested in using these data to estimate seasonal density, cohort structure, growth, mortality, and fecundity, as well as annual production and P/B of *M. diluviana* in 2013, and comparing those values to estimates from the 1990s.

Methods

Sample collection

Samples of *M. diluviana* were taken in Lake Ontario from April to November of 2013, using vertical net tows (Fig. 1; see also Appendix 1). Vessels and agencies involved included the United States Geological Survey (USGS) *RV Kaho* and *RV Lacustris* monthly from April-November; the Ontario Ministry of Natural Resources and Forestry (OMNRF) *RV Ontario Explorer* in April, May, July, September, and October, and also on their annual acoustic fish survey in July with the New York State Department of Environmental Conservation (DEC) *RV Seth Green*, the United States Environmental Protection Agency (EPA) *RV Lake Guardian* on biannual Water Quality Monitoring cruises in April and August, and lake-wide CSMI-year cruises in May, July, and September, and the Department of Fisheries and Oceans Canada

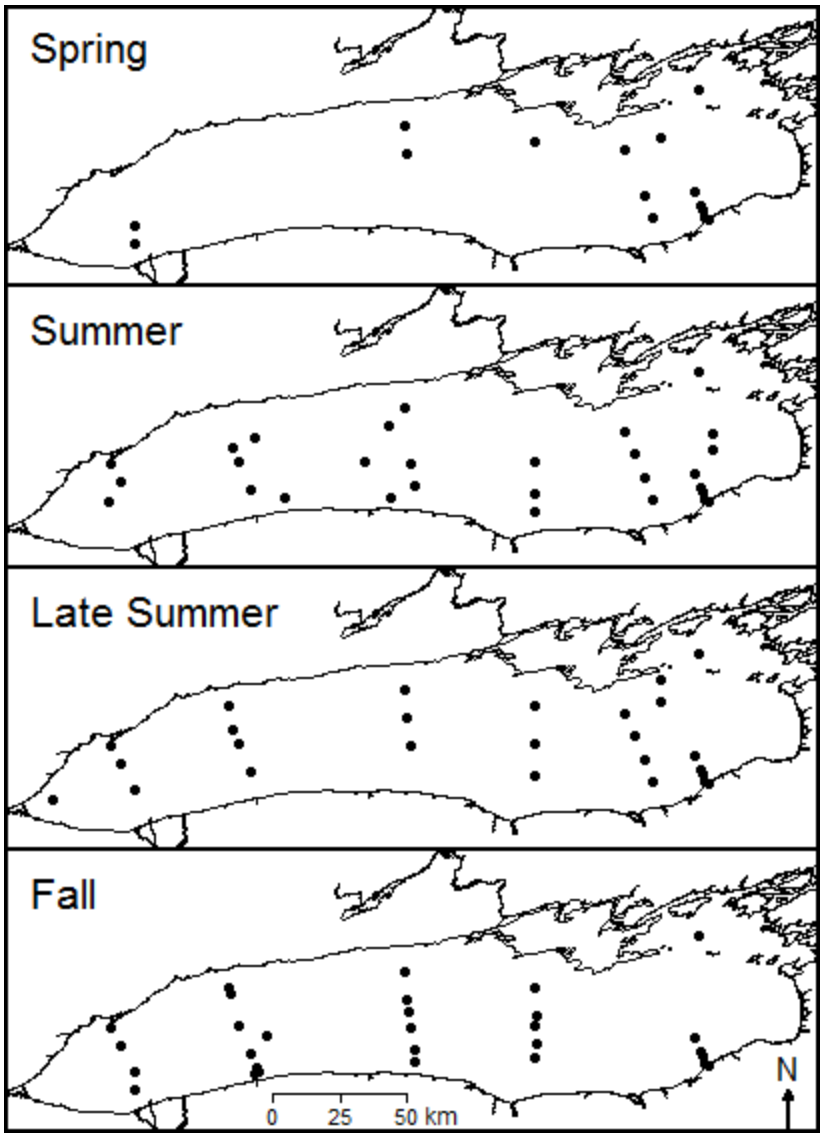


Figure 1. Map of sampling station coverage of Lake Ontario in each season (Spring: April 3 – May 28, Summer: June 10 – August 14, Late Summer: August 27 – September 11, and Fall: October 20 – November 20). Points are mysid sampling locations.

(DFO) *CCGS Limnos* and *CCGS Kelso* on their annual lake-wide survey in October and additional west-basin cruises in August and September. All survey crews conducted sampling for *M. diluviana* was at night between 1 hour after sunset and 1 hour prior to sunrise in order to capture *M. diluviana* that had migrated into the water column. To avoid repelling light-sensitive *M. diluviana*, survey crews conducted all sampling with red lights, turning off other deck-lights at least 10 minutes prior to sample collection.

Survey crews collected samples of *M. diluviana* by lowering large-mesh vertical plankton nets either to the very bottom of the lake (with net mouth 2-5 m above the bottom) or to 100 m (OMNRF/DEC annual acoustic fish survey in July). After resting nets at the tow depth for 30-60 seconds to allow *M. diluviana* to redistribute naturally (and to reduce probability of inverting the net), survey crews retrieved the nets at a rate of 0.5 m/s, and preserved sample contents in solutions of either ethyl alcohol (at least 70 %) or formalin (4-10 %). While vertical plankton net designs used by different survey crews varied, I consider these designs sufficiently similar to assume equivalent catchabilities. The EPA standard mysid net had a 1-m diameter mouth and was 2 m long, with the upper 2/3 of the net having 500 μm mesh, and the lower 1/3 and the cod end having 250 μm mesh. The USGS net had 1-m diameter mouth, and was 3 m long, with the entire net and cod-end having 1 mm mesh. The OMNRF and DFO nets had a 1 m x 1 m square mouth, and was 1.75 m long, with the upper 2/3 of the net having 1 mm mesh, the lower 1/3 having 250 μm mesh, and the cod-end having 64 μm mesh. Elsewhere, extensive comparison of 0.25 and 0.5 m diameter nets suggests little effect of net sizes on density and size estimates for *M. diluviana* (Silver et al., 2016).

Sample processing

For all surveys, analysts processed mysid samples for total count, size distribution, sex ratio, and reproductive status of males and females. All mysids in all samples were identified to species (mostly *Mysis diluviana*, a few *Hemimysis anomala)* and counted. Analysts measured a random subsample of 100 *M. diluviana* per sample. If there were fewer than 100 *M. diluviana* in a sample, all *M. diluviana* were measured. All mysid lengths were measured from the tip of the rostrum to the end of the abdomen (to the nearest 1 mm) using digital photographs and the program ImageJ. Sex and maturity was determined for all measured animals longer than 11 mm. Maturity was determined for females by the presence of brood in the marsupium (Tattersall and Tattersall, 1951). Females with translucent, distended brood lamellae but no young were recorded as "spent". All gravid females were separated, photographed, and measured and the number of embryos in the marsupium enumerated (except that some broods were not enumerated in the October survey, due to high numbers of gravid females in the net hauls). Maturity was determined for males by presence of bifurcate 4^{th} pleopods that extended beyond the posterior tip of the telson (Tattersall and Tattersall, 1951). Note that maturity of males was determined post-processing via visual assessment of photographs, and this has not yet been performed for samples from the Department of Fisheries and Oceans Canada (DFO) annual lake-wide survey in October. Also note that for a few samples (usually replicate tows), analysts recorded only the total count of *M. diluviana* present.

To calculate areal density for each station visit, I first divided the sample count by the area of the net mouth to calculate sample density ($\#/m^{-2}$). I then calculated the

individual mass of each measured mysid using the regression equation: ln (W, dry wt in g) = -12.27 + 2.72 ln (L, mm) (Johannsson, 1995; Johannsson et al., 2011), where L is the distance from the tip of the rostrum to the end of the abdomen, and calculated the mean individual mass of each sample. I calculated sample areal biomass as the product of mean individual dry mass and areal density of *M. diluviana* for each sample. For station visits with replicate samples, I averaged replicate areal density and biomass estimates to obtain one mean value per station visit. For samples with only total count data, I used the mean of pooled individual dry masses for all measured *M. diluviana* from the same station visit. For two station visits, no *M. diluviana* lengths were recorded from any of the samples, so I used the grand mean of mean individual dry mass for all other samples in the same season and depth zone (see below).

Lake-wide density and biomass

To calculate seasonal and annual lake-wide density and biomass, I first separated station visit estimates of density and biomass into groups by both date and bottom depth. I made four seasonal groups: Spring (April 3 – May 28), Summer (June 10 – August 14), Late Summer (August 27 – September 11), and Fall (October 20 – November 20). Within each seasonal group, I used five bottom-depth zones: 0-30 m, 30-60 m, 60-100 m, 100-150 m, and 150-250 m. For each bottom depth zone in each season, I calculated density and biomass (mean and SE). I used the proportion of Lake Ontario's surface area represented by each bottom depth zone to calculate lake-wide weighted density and biomass (mean and SE) for each season. I obtained the surface area of the lake within each depth zone from the National Geophysical Data Center's Bathymetry of Lake Ontario (1999). To determine the number of days represented by

each season, I calculated the mean Day of Year for each season based on the number of samples from each date as being May 8th, July 14th, September 8th, and October 27th, and found the number of days encompassed by the halfway points for these dates. This resulted in 130, 61.5, 52.5, and 121 days for Spring, Summer, Late Summer, and Fall periods, respectively. I then used the number of days represented by each season as seasonal weights to calculate annual lake-wide weighted density and biomass (mean and SE).

For both Spring and Summer, I used available data on zooplankton biomass to calculate the percentage of crustacean zooplankton biomass made up by *M. diluviana*. Zooplankton data were obtained from a dataset of samples collected by EPA Great Lakes National Program Office (GLNPO) and Cornell University during April and August of 2013. These samples were collected using a standard 153 μm mesh vertical plankton net towed from 100m to the surface (Rudstam and Watkins, *unpubl. data*).

I also compared my 2013 estimates of density and biomass to historical estimates. I obtained seasonal estimates of 100-150 m (station 41) densities and standard errors for 1971, 1972, and 1984-1995 from figure 3 in Johannsson et al. (2003). Johannsson et al. in turn had obtained 1971 and 1972 data from the dataset described by Carpenter et al. (1974), using data from only those samples collected at night. I used these data to calculate seasonally-weighted annual average densities for each of these years. I estimated fall lake-wide densities and standard errors for 1990, 1991, 1995, and 2002-2012 using DFO data (Johannsson et al., 2011, Rudstam et al., *in press*). I obtained the estimate of year-average lake-wide density and standard error for 1990 using data from figure 5 of Johannsson (1995). I used size structure and density estimates for 50

m depth zones in Lake Ontario in 1990 and 1995 (Johannsson, 1995; Bowen and Johannsson, *unpublished data*) to calculate lake-wide, seasonally-weighted annual average biomass for 1990 and also lake-wide annual density for 1995. Note that I was unable to calculate a standard error for the lake-wide estimate for 1995 because I lacked error estimates for depth-specific mean densities. I determined statistical inference of significant pairwise differences between the 2013 estimates of density and those from earlier years by comparing overlap of the 95% confidence limits of 2013 with the mean of each other year and also the mean of 2013 with the 95% confidence limits of each other year.

Life history

I constructed 1-mm length-frequency distributions ($x \leq \text{length} < x+1$) for each station visit, and used these length-frequency distributions to determine cohort structure. I averaged length-frequency distributions of replicate samples by size bin so that there was only one length-frequency distribution per station visit. I named annual cohorts as follows: animals released from the brood pouch in 2013 were the age-0 cohort in 2013 (and the age-1 cohort in 2014), animals released from the brood pouch in 2012 were the age-1 cohort in 2013 (and the age-0 cohort in 2012), and animals released from the brood pouch in 2011 were the age-2 cohort in 2013 (and the age-1 cohort in 2012).

To assess cohort development, I used a finite Gaussian mixed model approach to fit the sum of a fixed number of normal distributions (one for each cohort) to the observed size distribution in each station visit. I restricted the fit of the mean length

for each cohort to be within a predetermined range for each cohort and season. I determined that range from inspections of the size structure at all station visits for that season. I used the optim() command in R to find the solution that minimized the sum of squared deviations (R Core Team, 2014). This procedure gave me the mean length, standard deviation of lengths, and relative density of each cohort for each station visit. I used these to calculate the seasonal lake-wide density of each cohort (weighting cohort density according to bottom depth zones as described in *Lake-wide density and biomass* section), which I used to calculate the proportion of *M. diluviana* in each cohort during each season. To visualize seasonal patterns in lake-wide cohort development and population demographics, I calculated seasonal lake-wide 1-mm size-frequency distributions (again, weighting size bin density according to bottom by depth zones as described in *Lake-wide density and biomass* section).

For each season, I calculated the lake-wide proportion of the age-1 cohort made up by juveniles, immature males, mature males, non-gravid females, spent females (grouped with non-gravid females), and gravid females using a multi-step process. The first step involved enumerating the number of animals in each of those demographic groups which were also members of the age-1 cohort. I did this for each sample on a size-bin by size-bin basis. For each size bin, I could calculate the proportion of the individuals from the size bin which belonged to each cohort based on a comparison of the individual cohort distributions from the finite Gaussian mixed model fit. When more than 95% of the animals in a size bin belonged to either the age-1 or the age-0 cohort, I considered all the animals in that size bin to be members of that cohort. Then, the total number of animals in each cohort was calculated as the sum of the animals in

that cohort across all size bins. The number of animals in the age-1 cohort was further divided into different demographic groups based on the number of *M. diluviana* belonging to each demographic group in each size bin. For each of these demographic groups, I extrapolated up to the seasonal lake-wide density according to the methods described in the *Lake-wide density and biomass* section above. Finally, I calculated the seasonal lake-wide proportions of each demographic group within the age-1 cohort from these density estimates.

I also calculated the lake-wide mean number of embryos per gravid female and the lake-wide mean gravid female length. For each season, I calculated the former as the weighted grand mean of the mean number of embryos per gravid female in each bottom depth zone, and I calculated the latter as the weighted grand mean of the mean length of gravid females in each bottom depth zone. I determined the weights of each bottom depth mean as the product of the mean density of gravid females and the total surface area of each bottom depth zone. I also fit the number of embryos per gravid female as a function of female length with four linear least-squares regression models (separate regressions for each season).

I estimated daily growth rates for each cohort by plotting mean cohort length (mm) for each visit as a function of Day of Year, and fitting a linear least-squares regression for each cohort. Note that growth rate estimates are based on data for each station visit rather than seasonally-pooled summaries. Over-winter growth was estimated using the 2012 fall size distribution (Bowen, unpublished data). I estimated mortality for each cohort from the slope of the regression of ln(lake-wide cohort density) as a function of time (mean Day of Year for seasons, see *Lake-wide density and biomass* section). For

comparison, I obtained growth rate estimates from Johannsson (1992, 1995), and determined significance of pairwise differences between years by comparing overlapping of 95% confidence intervals (mean +/- 2 SE) with pairwise means.

I used linear least-squares regression of the log-cohort densities at each season to calculate mortality. Because the error and significance of the mortality rates generated by a linear least-squares regression using just the 4 seasonal points reflected neither the number of samples nor the level of confidence I have in each seasonally-pooled estimate of lake-wide density, I used a bootstrapping method to obtain confidence limits for these mortality rates. I generated 10,000 independent data points for each cohort and season according to random normal distributions with the observed means and standard errors of seasonal cohort densities. For each cohort, I randomly grouped these data into 10,000 sets of Spring – Fall lake-wide density estimates. For each set, I calculated 10,000 mortality rate estimates. I then arranged each cohort's mortality slope estimates in order from lowest to highest, taking the 250^{th} and $9{,}750^{th}$ estimates as the 95% confidence limits of the mortality rate estimate and of the model fit for the cohort.

Production

I estimated annual production according to the Hynes size-frequency method as modified by Menzies (1980). This method has been commonly used for calculating production of mysid populations, including *Mysis diluviana* (Sell, 1982; Johannsson, 1992, 1995; Caldwell and Wilhelm, 2012). The method sums biomass lost between size classes over the course of a year to calculate production (P):

$$P = \sum_{j=1}^{i}(N_{j+1} - N_j) \cdot (W_j W_{j+1})^{1/2} \quad \text{Eq. 1}$$

$$\text{and } N_j = i \cdot \bar{n}_j \cdot Pe_j/Pa_j \cdot 365/CPI \quad \text{Eq. 2}$$

where i = number of size categories, N_j = the number of *M. diluviana* that developed into size category j in a year, W_j = mean weight of *M. diluviana* in category j (calculated as the geometric mean of weight at the upper and lower bounds of size category j), $\bar{n}_j$ = mean number of *M. diluviana* in category j over the course of a year, Pe_j = estimated proportion of the life cycle spent in category j (1/i), Pa_j = actual proportion of the life cycle spent in category j. When j = i, $N_{i+1} = 0$ and W_{i+1} = weight at maximum size observed. I estimated Pa_j using each cohort's calculated daily growth rates up to October 28, the estimated daily over-winter growth rate from October 28 to April 2 (based on sizes from 2013), and the next cohort's daily growth rate through October 28. The CPI or cohort production interval equals the number of days from hatching to reaching the largest size class, and was set as the number of days required to reach the largest size observed given observed growth rates (893 days for this study).

Where N_j values have been underestimated, this method of calculating production can result in a negative "$N_{j+1} - N_j$," and thus negative production between two size classes. For *M. diluviana*, this usually occurs for the smallest size classes (< 5mm) and size classes of the first overwinter period (~9-13mm; Johannsson 1995). One way to remove this negative bias in the production estimate is to exclude the N_j and W_j values for the underestimated size classes when calculating production according to the Hynes-Menzies equation (Eq. 1). For the intervals containing underestimated N_j

estimates, the difference in N_j and geometric mean of W_j are calculated between the size classes on either side of the underestimated size classes. Note that sometimes more than one size class must be removed to avoid negative bias in the production estimate. This process uses the N_j and W_j estimates on either side of the underestimated portion of the size frequency distribution to estimate the actual N_j and W_j for the size classes where N_j was underestimated. This method of removing negative bias has been employed for calculating production of *M. diluviana* populations in the past (Johannsson, 1995, *pers. comm.*).

Krueger and Martin (1980) describe a formula for calculating the variance of the Hynes size-frequency production estimate, which I include below in a form appropriately modified to match the Menzies (1980) modification of the Hynes size-frequency method:

$$v(\mathrm{P}) = \mathrm{G_1}^2 \cdot v(\mathrm{N_1}) + \sum_{\mathrm{j}=2}^{\mathrm{i}} \left(\mathrm{G_j} - \mathrm{G_{j-1}}\right)^2 \cdot v\left(\mathrm{N_j}\right) \qquad \text{Eq. 3}$$

$$\text{and } v(\mathrm{N_j}) = \mathrm{i}^2 \cdot v(\bar{\mathrm{n}}_\mathrm{j}) \cdot \left(\mathrm{Pe_j}/\mathrm{Pa_j}\right)^2 \cdot (365/\mathrm{CPI})^2 \qquad \text{Eq. 4}$$

Where G_j is $(W_jW_{j+1})^{1/2}$. When j = i, $G_i = (W_iW_{i+1})^{1/2}$, and W_{i+1} is as described above for Eq. (1). This variance equation (Eq. 3) must also exclude the same N_j and W_j values as Eq. (1) when correcting for underestimated N_j estimates, and requires an additional change as well in Eq. (4). Since the confidence in the production estimate is based on the number of size bins contributing actual N_j estimates to the estimate of P in Eq. (1), the contribution to the total variance (v(P)) of the variance in each size class ($v(N_j)$) must be scaled according to the number of size classes actually used. This means the value for i in the calculation of $v(N_j)$ (Eq. 4) must be set to i' = i - k, where

k is the number of size bins with underestimated N_j values which are being excluded during the calculation of P (Eq. 1) and *v*(P) (Eq. 3). This adjustment does not affect the calculation of N_j in Eq. (2). For that equation, the missing N_j values are estimated by the N_j values which are still present, which assumes the utilized N_j values were accurate when calculated according to the number of size classes originally present (i) and the expected amount of time spent in each of those original size classes (Pe_j). For the same reason, this does not change the calculation of the ratio of expected and actual time spent in each of the utilized size class (Pe_j and Pa_j) for Eq. (2) and Eq. (4).

I estimated production at the spatial scales of the whole lake and of the 100-150m zone. Note that as I apply it, these calculations of production assume a stable population because they estimate over-winter mortality and growth based on Fall and Spring size structures observed in 2013 alone. I calculated P/B by dividing production (g dw/m^2/yr) by average annual biomass (g dw/m^2; see *Density and biomass* section).

I also compared my estimates to historical production estimates. I obtained estimates of 100-150m production for 1984-1995 from figure 7a in Johannsson et al. (2003), lake-wide production for 1990 (assuming 100% net efficiency and accounting for underestimation of August densities) from Johannsson (1995), and 50-250m production for 1995 from Johannsson et al. (2011). I converted the 50-250m production estimate to lake-wide production by assuming no production in the 0-50m zone as in 1990. Since the area of Lake Ontario in the 50-250 zone is 0.68 of the total area, lake-wide production is 0.68 of 50-250m production. I consider this assumption valid because *M. diluviana* production in the 0-50m zone in 1990 was negligible enough to result in the same lake-wide estimate of production for that year as if 0 g

dw/m^2/yr had been assumed for the 0-50m zone (see Johannsson, 1995; Table 6). I further converted the 1995 production estimate to maintain the assumption of 100% net efficiency by multiplying it by 0.87 (the net efficiency assumed by Johannsson, 1995). I compared my estimates of average production and P/B in 2013 with historical values. I considered my estimate of annual production in 2013 to be significantly different from an estimate for a previous year if the previous year's estimate did not fall within the 95% confidence limits I estimated for production in 2013.

Results

Density and biomass

Areal density and biomass displayed strong depth-dependent relationships in all seasons (Table 1; Appendix 1). Densities increased from 0-22 /m^2 in the 0-30 and 30-60 m depth intervals to over 330 /m^2 in 150m and deeper water (Spring, Summer, and Late Summer values). The increase (with bottom depth) was dramatic at 60 m to 100 m, similar to previous findings (Johannsson, 1995; Rudstam et al., 2008; Watkins et al., 2015). Lake-wide densities and biomasses were highest in the Late Summer and lowest in Spring and Fall (Table 1). Year-average density was 99 /m^2 (SE = 11) for the whole lake and 126 /m^2 (SE = 15) for the 100-150m zone. Year-average biomass was 319 mg/m^2 (SE = 28) for the whole lake and 494 mg/m^2 (SE = 55) for the 100-150m zone. *M. diluviana* represented 24.2% and 11.0% of the total crustacean zooplankton biomass in Spring and Summer, respectively. All three measures of density in 2013

Table 1. Density (mysids/m^2) and biomass (mg dw/m^2) by season and depth zone (m bottom depth), with standard errors and ranges.

Period	*Depth Zone*	*n*	*Density*	*range*	*Biomass*	*range*
Spring	0-30	3	5 *(5)*	0 – 15	0.7 *(0.7)*	0 – 2
	30-60	5	22 *(13)*	3 – 73	40 *(17)*	7 – 85
	60-100	5	47 *(36)*	3 – 190	178 *(145)*	21 – 759
	100-150	7	116 *(33)*	37 – 283	324 *(99)*	85 – 868
	150-250	3	337 *(73)*	191 – 423	744 *(184)*	437 – 1073
	Lake-wide		107 *(17)*		262 *(51)*	
Summer	0-30	6	0 *(0)*	0 – 0	0 *(0)*	0 – 0
	30-60	3	5 *(4)*	0.7 – 13	22 *(20)*	0.2 – 62
	60-100	7	46 *(9)*	15 – 78	233 (*72)*	79 – 488
	100-150	15	143 *(23)*	41 – 387	486 *(62)*	148 – 891
	150-250	11	360 *(75)*	141 – 942	875 *(295)*	272 – 3678
	Lake-wide		114 *(35)*		333 *(62)*	
Late	0-30	4	0.1 *(0.1)*	0 – 0.3	0.4 *(0.4)*	0 – 1
Summer	30-60	4	9 *(3)*	0 – 14	31 *(14)*	0 – 54
	60-100	6	70 *(21)*	16 – 153	372 *(116)*	65 – 729
	100-150	11	162 *(22)*	74 – 272	840 *(111)*	358 – 1465
	150-250	6	383 *(81)*	138 – 638	993 *(186)*	430 – 1449
	Lake-wide		128 *(17)*		466 *(50)*	
Fall	0-30	2	4 *(0)*	4 – 4	4 *(2)*	2 – 6
	30-60	4	0 *(0)*	0 – 0	0 *(0)*	0 – 0
	60-100	7	33 *(12)*	0 – 84	123 *(41)*	0 – 268
	100-150	8	113 *(23)*	5 – 220	530 *(112)*	15 – 1047
	150-250	8	182 *(32)*	71 – 331	817 *(207)*	170 - 1734
	Lake-wide		69 *(19)*		308 *(49)*	

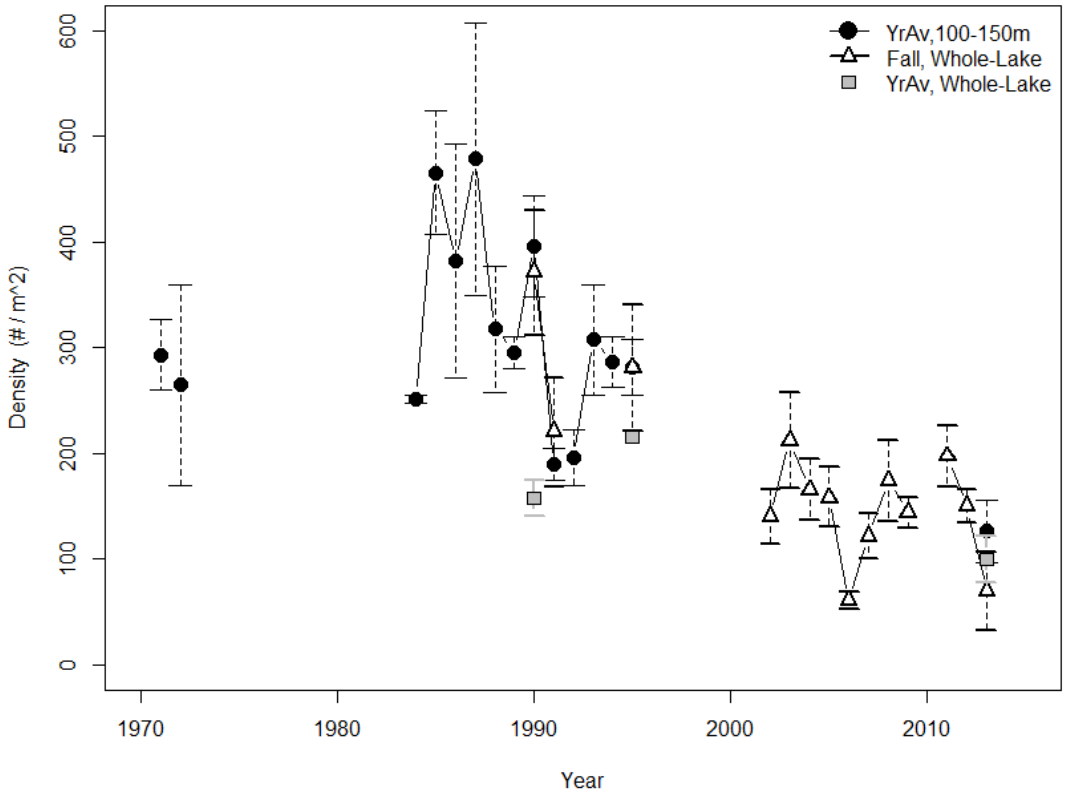


Figure 2. Density (areal density ± 2 SE) of *Mysis diluviana* in Lake Ontario from the 1970s to 2013. Year-Average data are seasonally weighted estimates from samples taken throughout the year, mostly for the 100-150m bottom depth region. Fall data are estimates from samples taken in October-November. Lake-wide data are depth-weighted estimates from samples taken across the lake basin.

(year-average whole lake, year-average 100-150m zone, and Fall whole lake) were significantly lower (by 30-80%) than values for the same three measures as estimated for the period 1984-1995. The Fall lake-wide density estimate for 2013 was also significantly lower than Fall lake-wide density estimates for 2000 to 2012, except for the low estimate for 2006 (Fig. 2).

In addition to *M. diluviana*, I also detected a few individuals of *Hemimysis anomala* at a 5-m USGS station off of Oswego, NY in samples collected on August 7th and on November 21st. In the August sample, I found one juvenile at 3.4 mm length; 1 juvenile, 2 males, and 3 females at 4-5.5 mm length; and one gravid female at 7.2 mm length carrying 19 early-stage embryos. In November, I found two juvenile *H. anomala* at 4 mm length, which co-occurred with three juvenile *M. diluviana* (at 3.3, 5.6, and 6.3 mm).

Life history

Two cohorts were present throughout the year: animals released in 2013 (age-0 cohort) and animals released in 2012 (age-1 cohort). I found little overlap in the length distribution of the two cohorts in Spring and Summer, but the overlap increased in Late Summer and Fall (Fig. 3). Very few small (< 6 mm) animals contributed to the Fall cohort structure in 2013 (Fig. 3). The percent of males to females in the age-1 cohort was 51-54% throughout Spring to Late Summer periods and decreased to 32% in the Fall. Gravid females were at the highest densities in Fall, and these females were longer and had larger broods than gravid females in other seasons (Table 2). Nearly all gravid females observed in 2013 were the length of age-1 animals when

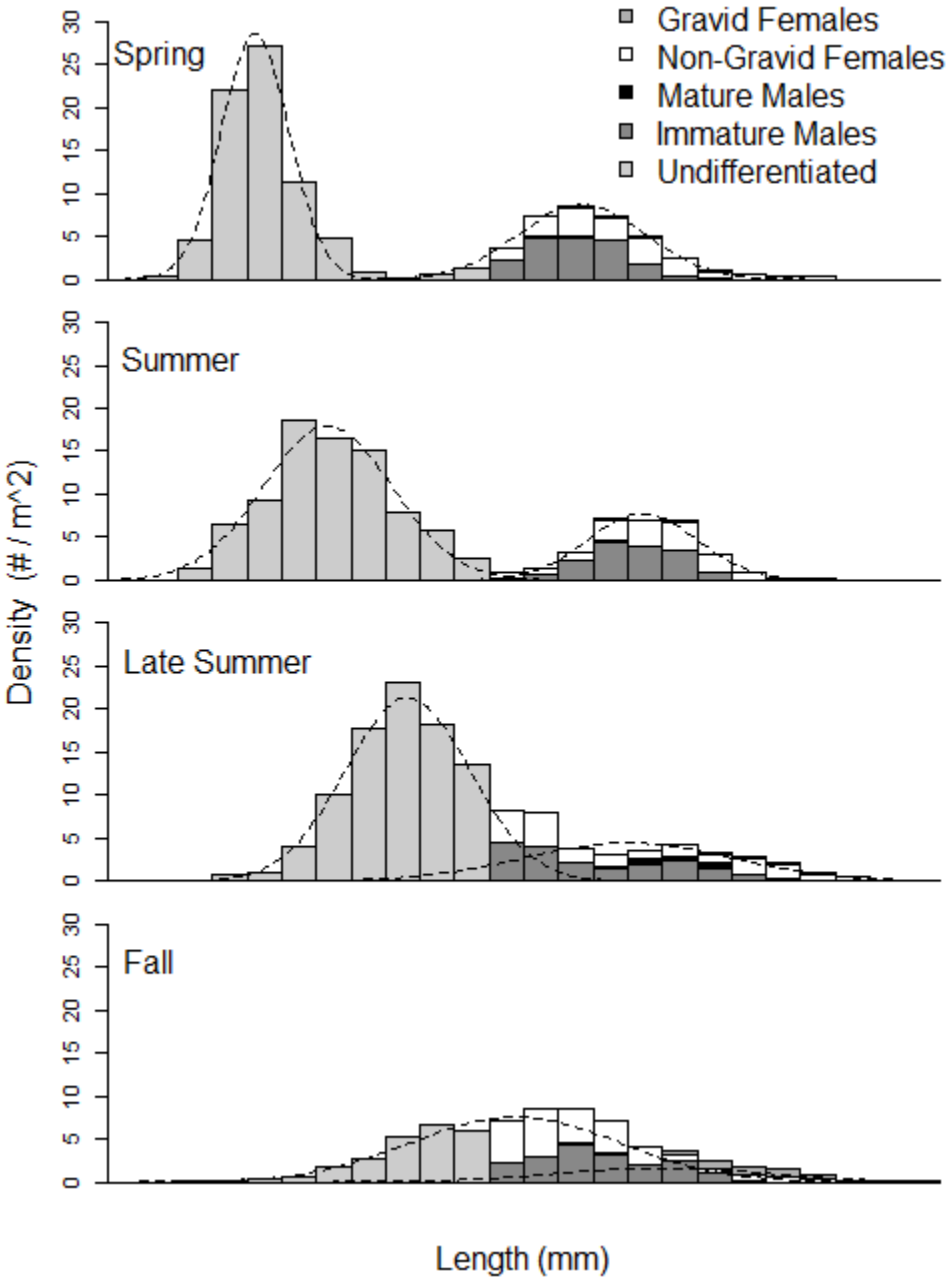


Figure 3. Length-density barplots for each season in 2013 (seasons defined in Fig. 1). Lengths in mm from tip of rostrum to end of abdomen; bins are ($x \leq$ length $< x+1$). Shading represents different life stages (see legend). Spent females were rare and binned with non-gravid. Fits of finite Gaussian mixed models are plotted for each season as dashed lines to illustrate fit used for each station visit (see *Life history* section of Methods for *Chapter 2*). Note that I did not determine maturity for males in October, yet mature males likely made up 30-50% of age-1 males in the Fall (see *Life history* section of Results for *Chapter 2*).

Table 2. Lake-wide seasonal age structure and demographic data, as weighted by bottom depth zone: the percent of the *M. diluviana* population in age-0 and age-1 cohorts in 2013; the percent of age-1 mysids which were smaller than 11 mm (Juv), were male (♂), and were female (remaining); percent of age-1 males that were mature (♂ Mat) and of age-1 females that were gravid (♀ Grv); mean length of gravid females (Grv mm), mean number of embryos per gravid female (Emb/Grv), and mean embryo density (Emb/m^2). See *Life History* section of Methods for *Chapter 2* for determination of life stages and for calculations. Data from the lake-wide October do not currently specify maturity of male *M. diluviana*. However, analysis of a few photographs of samples indicate they are likely to have been high (30-50%, Bowen, *pers. comm.*; Holda, *pers. obsv.*). For Fall I instead report the percent of age-0 male *M. diluviana* which were mature based on USGS survey in November.

	Percent of Density		*Percent of age-1*						
Period	*age-0*	*age-1*	*Juv*	♂	♂ *Mat*	♀ *Grv*	*Grv mm*	*Emb/Grv*	*Emb / m^2*
Spring	64.7	35.3	5.8	48.4	1.8	4.0	15.1	13.4	9.5
Summer	72.8	27.2	4.1	50.1	0.8	2.0	16.1	13.3	3.7
Late Summer	81.1	18.9	3.5	51.9	18.3	7.9	17.7	30.0	25.2
Fall	87.6	12.4	0.3	32.1	11.5*	67.7	18.4	31.7	124.5

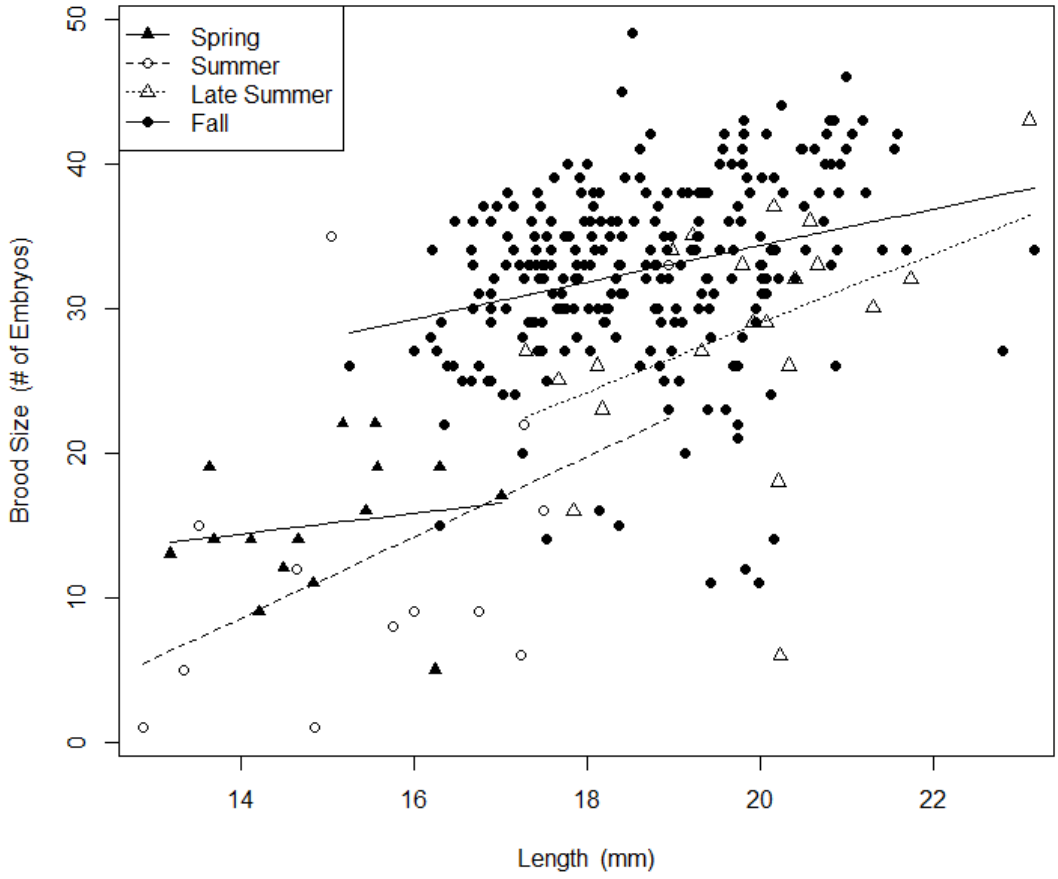


Figure 4. Brood size as a function of gravid female length and season (seasons defined in Fig. 1). Each point represents one individual gravid female, and lines represent best-fit linear regressions. Point and line styles are by season (see legend).

observed. Thus, gravid females I observed in the Spring likely mated in the late fall or winter of 2012 while still age-0 individuals (Fig.4; see also Appendix 2). Only three gravid females observed (in October) were possibly from the age-0 cohort based on their length. However, it is likely they were small age-1 gravid females, as age-0 gravid females tend to become mature in late fall or winter (Bowen, *pers. comm.*). It is also possible they represent the small portion of the population that would have been released from the brood pouch in late summer of 2012. Only a small number (7-14) of larger females were caught in 2013 which were possibly from the 2011 cohort (see Appendix 2). If they were released in 2011, it is likely they were released in late summer of that year. The proportion of age-1 males that were mature increased sharply in Late Summer (Table 2). In the Fall, I observed the occurrence of a few small mature males from the age-0 cohort. These males had matured about 7 months after release from the brood pouch (Table 2). Between 30% and 50% of age-1 males in October were likely mature, based on analysis of some photos (Bowen, *pers. comm.*; Holda, *pers. obs.*). *M. diluviana* maturing as age-0 individuals did so later in the Fall than *M. diluviana* maturing as age-1 individuals.

The growth rates of *M. diluviana* in 2013 were different from those observed in Lake Ontario during the 1980s and 1990s. Age-0 mean cohort length did not increase linearly with time. Therefore, I estimated daily growth for this cohort by fitting a piecewise linear least-squares regression with the segmented() function from the segmented package for R (Muggeo, 2008). The piece-wise regression was a better fit than the simple regression when comparing residuals and AIC scores (ΔAIC = 14.9). Age-0 Spring-Summer growth estimates are not reliable because the apparent slow

Spring growth is likely due to a combination of continued release of young and perhaps low selectivity of the gear for the smallest sizes classes. Therefore, I only used the Summer – Fall portion of the piecewise regression for my estimation of mean age-0 *M. diluviana* growth rate in 2013. I also excluded two outliers from the age-0 regressions. These two points had high leverage and were made up by only 2-3 individuals each, collected from 5 m and 20 m USGS stations off of Oswego, NY in November. The age-1 mean cohort length data met the assumptions of normality and homogeneity of variance required for linear least squares regression. Calculated daily growth rates were 0.052 mm/d (SE: 0.003) for age-0 *M. diluviana*, and 0.026 mm/d (SE: 0.003) for age-1 *M. diluviana* (Fig. 5). Previously estimated growth rates from the 1980s and 1990s are 0.035 mm/d for age-0 and 0.029 mm/d for age-1 (Johannsson, 1992, 1995), representing significantly higher growth rates in 2013 for age-0 *M. diluviana* (not significant for age-1). Daily over-winter growth rates for transition from age-0 to age-1 were estimated to be0.022 mm/d (from 2012 fall to 2013 Spring) and 0.014 mm/d (from 2013 Fall to 2014 spring). However, the latter estimate is uncertain because the length distribution of age-1 in spring 2014 is from two samples at one station (station 41; 130 m).

I estimated mean mortality rate of age-0 *M. diluviana* using only Summer, Late Summer and Fall estimates of cohort density, as was done for growth rates. My estimates of instantaneous daily mortality were 0.003 (SE: 0.004, 95% CI: -0.001 to +0.007) for age-0, and 0.008 (SE: 0.003, 95% CI: -0.004 to -0.012) for age-1 (Fig. 6).

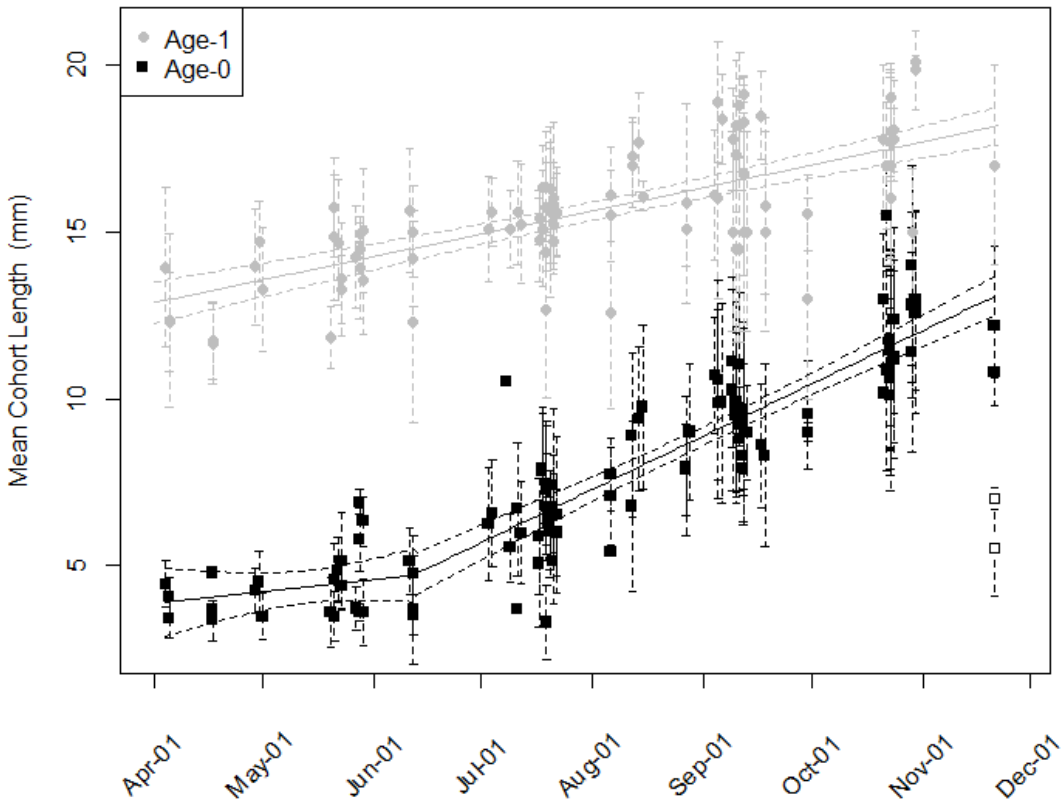


Figure 5. Mean cohort length (to end of abdomen) from finite Gaussian mixed model fits versus visit date for each station visit. Symbols represent age-0 and age-1 cohorts, and error bars for each data point represent one standard deviation (from finite Gaussian mixed model fit). Regressions for growth rates were performed separately for each cohort, and are given with ± 2 SE (dashed lines). Age-0 growth was better fit by a piece-wise linear regression (ΔAIC = 14.9). Two outliers (open squares) were excluded from age-0 regression.

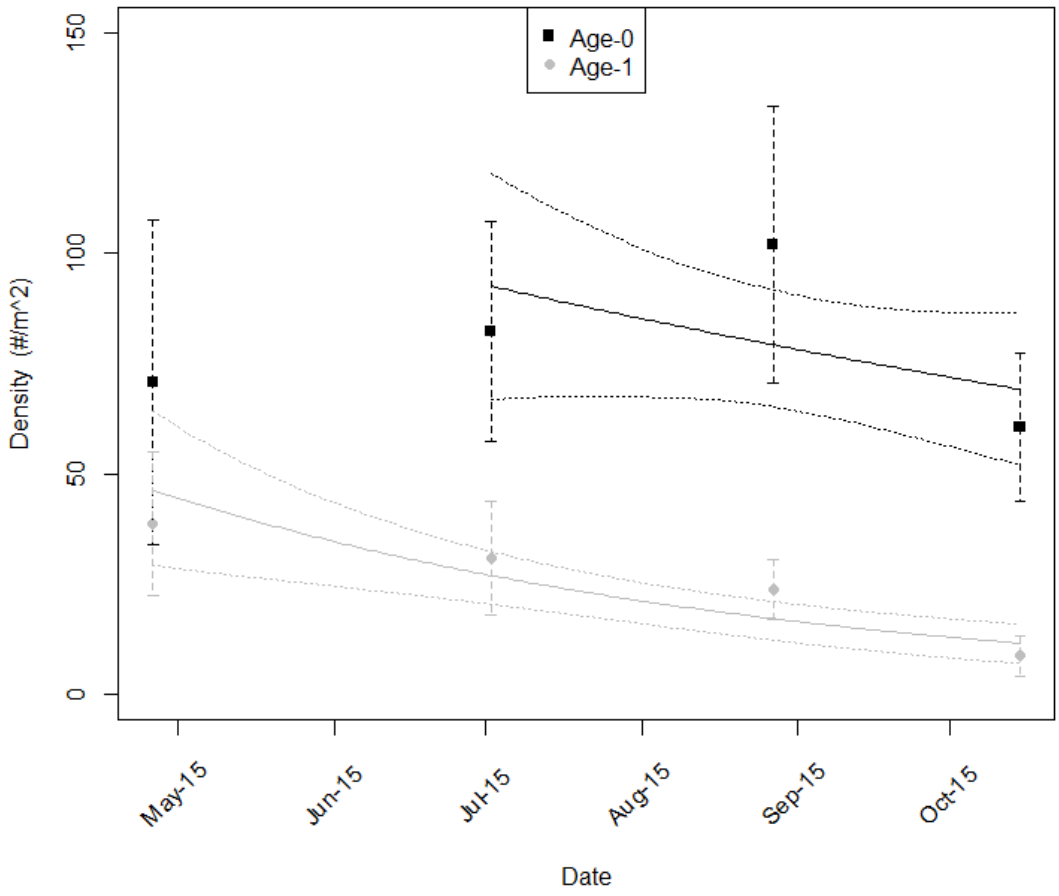


Figure 6. Lake-wide seasonal densities of age-0 and age-1 cohorts in 2013 ± 1 SE. Lines are derived from the regression of ln(density) versus date. Dotted lines represent 95% confidence intervals of model fit.

Production and P/B ratio

Lake-wide production of *M. diluviana* was 0.85 g/m^2/yr (SE: 0.03) in 2013. This results in a lake-wide average P/B of 2.65 /yr (given observed mean annual biomass of 319 mg dw/m^2). Production was higher in the 100-150 m zone, at 1.22 g/m^2/yr (SE:.0.05). This results in a 100-150 m P/B of 1.71 /yr (given observed annual average biomass of 494 mg dw/m^2). Production in 2013 was significantly lower than production in the 1990s (about 35%, Fig. 7). My estimate of P/B for 2013 is about 15-20% lower than previous estimates of P/B for 1990 and 1995 (from 3.11 /yr and 3.24 /yr to 2.65 /yr). I do not have an error estimate for P/B in 2013, and so cannot address the statistical significance of this difference.

Discussion

This study is the first to estimate lake-wide annual production of *M. diluviana* in Lake Ontario after the ecological changes of the 1980s and 1990s associated with oligotrophication and dreissenid mussels (Mills et al., 2003). *M. diluviana* density and biomass have declined substantially since the mid-1990s, and were at a near all-time low in 2013. On the other hand, age-0 growth rate, age-1 length at age, and mean brood size per gravid female increased compared to the 1990s. I also observed reproduction in a few age-0 males (indicating minimum generation times have shortened since the 1990s) and near-absence of the Late Summer cohort. These increases in individual growth and reproduction rates should lead to an increase in the

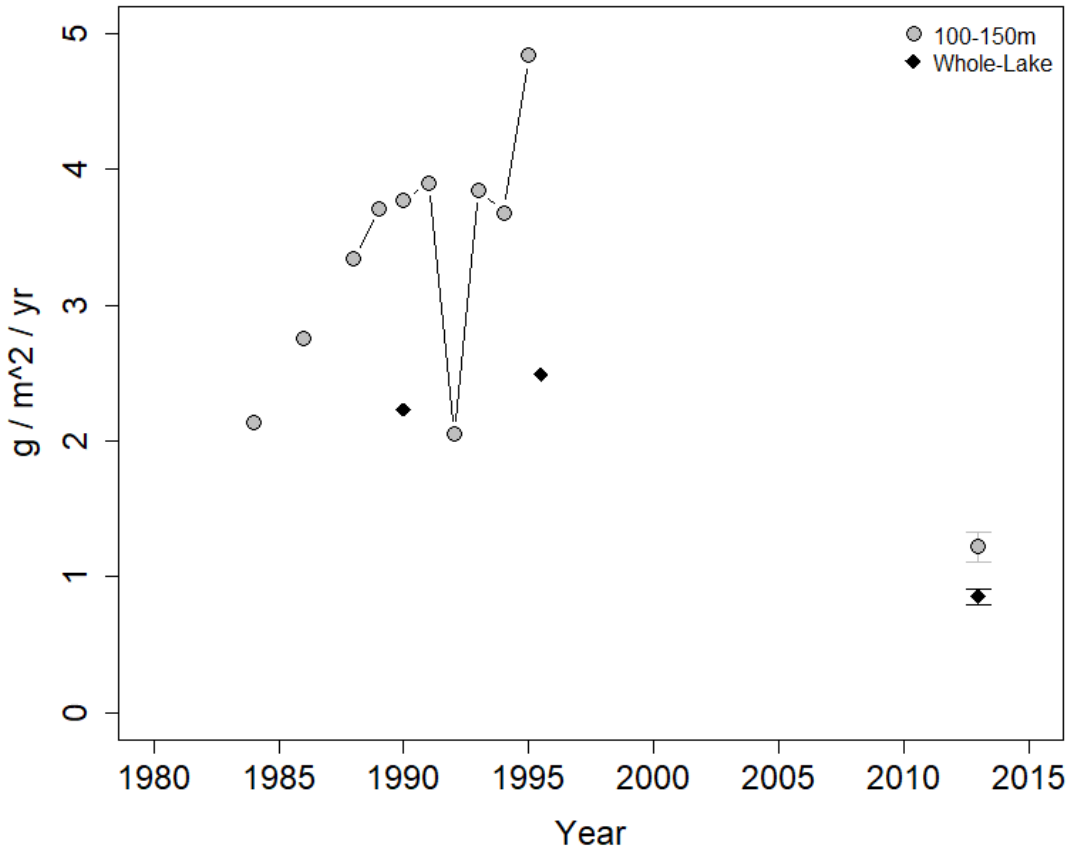


Figure 7. Historic annual production of *Mysis diluviana* in Lake Ontario plotted as areal dry-weight production versus year. Error bars for points are two standard errors and are only available for the 2013 data. See *Production* section of Methods for *Chapter 2* for historical data sources.

P/B ratio. However, I calculated a 15-20% decrease in P/B from 1990 and 1995 to 2013. Note that the uncertainty in this estimate is unknown.

Are the observed declines in *M. diluviana* density since the 1990s due to food limitation? The decline in *M. diluviana* density through time mirrors the decline in several other biological time series in Lake Ontario, including nutrient concentrations, epilimnetic chlorophyll concentrations, and epilimnetic zooplankton biomass (Dove and Chapra, 2015; Rudstam et al., *in press*). Similarly, increases in predatory cladoceran abundance have been correlated with declines in epilimnetic zooplankton abundance which were in turn correlated with declines in age-0 *M. diluviana* growth and abundance (Johansson et al., 2011). This led Johannsson et al. (2011) to hypothesize that competition between *M. diluviana* and the invasive predatory cladocerans was important for the observed declines in *M. diluviana*.

However, simultaneous with declines in algal production and epilimnetic zooplankton biomass, a greater proportion of primary production occurred in the deep chlorophyll layer, and zooplankton abundance in the deep chlorophyll layer increased (Scofield et al. 2017, Watkins et al. 2017). Since this deeper layer is where *M. diluviana* feed, it is questionable whether declines in total production reduced food availability for *M. diluviana*. Invasive predatory cladocerans may compete with *M. diluviana* for food, but they are also a source of food for *M. diluviana*. *M. diluviana* selected for *Cercopagis pengoi* in 2013 (O'Malley et al., 2017), and have been observed to eat *Bythotrephes longimanus* (Bowen, *pers. comm.*). So, it is questionable whether the arrival of invasive predatory cladocerans reduced or increased the food available for *M. diluviana*. These mitigations to potential food limitation are consistent

with my observations of increased growth rate of age-0 *M. diluviana* and of increased length-at-age and fecundity of age-1 *M. diluviana*.

My observations of increased growth and fecundity and reduced abundance of *M. diluviana* indicate increased mortality rates, presumably through predation, are the likely cause of decreased population size. Alewife (*Alosa pseudoharengus*) are known *M. diluviana* predators in Lake Ontario and their feeding rates on *M. diluviana* may have increased due to disappearance of *Diporeia* sp. (Walsh et al., 2008; Stewart et al. 2009, but see Riha et al., *in review*). Increasing water clarity may also have caused a shift in predator diets to include more *M. diluviana* (Boscarino et al., 2010). Another potential cause of increased predation is the arrival of round goby (*Neogobius melanostomus*) as a novel predator, which would likely feed on *M. diluviana* when *M. diluviana* are on the bottom, especially during the winter (Walsh et al., 2007; Weidel et al., *unpubl. data*).

Another notable change observed in the *M. diluviana* population in 2013 was the lack of small *M. diluviana* (<6mm) in the Fall. This suggests the dominance of a spring release period and the near absence of a late summer release period in 2013. This is in contrast to the two release periods observed in cohort development patterns during the early 1970s and the 1990s. Just as in 2013, cohort development in 1971 and the 1990s was dominated by fall reproduction and spring release, but there was a greater relative importance of the late summer cohort in 1971 and the 1990s. Patterns similar to that observed in 2013 have been observed in 1985 and in the 2000s (Shea and Makarewicz, 1989; Johannson, 1992; 1995; Johannsson et al., 2011). This suggests a dominant spring release may be the current norm. However, some years

still show substantial late summer releases of young *M. diluviana* (seen in 2012, Bowen, *unpubl. data*).

I observed a seasonal pattern of low densities of *M. diluviana* in Fall and Spring periods, and high densities in the Late Summer period. The lower density in the Fall is partially due to the high mortality of age-1 males after reproduction (Table 2), but also due to high mortality in the age-0 cohort (Fig. 6). The underestimate of density in the Spring may be due to differences in spatial coverage (Fig. 1), partial migration into the water column (Euclide et al., 2016), and/or continued recruitment of young to the sampling gear through May-June (some females were carrying embryos in April-May, and nets may have lower selectivity for smallest juveniles).

In conclusion, I show a decline in lake-wide abundance, biomass, and production of *M. diluviana*, and an increase in mean growth rate for age-0 *M. diluviana* and in length-at-age and fecundity for age-1 *M. diluviana* in 2013 compared to the 1980s and 1990s. This suggests an increase in foraging potential and predation risk since the 1990s. These observed declines in biomass and production of *M. diluviana* are a concern for prey fish production in Lake Ontario and the ability of the lake to support an increase in coregonids, which is one of the fish community objectives for the lake (Stewart et al., 2013).

APPENDICES

APPENDIX 1

Metadata and densities for all visits to all stations where *M. diluviana* samples were collected in Lake Ontario in 2013, with date (dd-mmm), survey crew, station name, latitude (decimal degrees), longitude (decimal degrees), station depth (m), number of net tows taken at station (and in parentheses the number of samples where *M. diluviana* were measured for biomass), average tow depth (m), areal density (#/m^2) of *M. diluviana* with SD, and areal biomass (mg dw/m^2) of *M. diluviana* with SD. Mean density and biomass values reported here are those used in analyses. Abbreviations for survey crews and details on net mouth area, dimensions, and mesh size can be found in the *Sample collection* section of Methods for *Chapter 2*.

Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
11-Jun	DFO	CSMI_040	43.59	-78.01	180	178	2 (1)	200	17	273	23
12-Jun	DFO	DFO_009	43.59	-79.39	63	61	2	15	14	77	75
12-Jun	DFO	DFO_013	43.42	-79.40	106	104	2	119	49	148	62
03-Jul	DFO	DFO_403	43.59	-78.22	178	176.5	4 (1)	141	14	295	29
04-Jul	DFO	CSMI_012	43.50	-79.35	111	109	4 (1)	53	5	210	20
14-Aug	DFO	CSMI_012	43.50	-79.35	107	107.3	3	123	13	468	50
15-Aug	DFO	DFO_009	43.59	-79.39	63	61	3	28	13	81	39
28-Aug	DFO	CSMI_019	43.38	-79.29	106	104	2	117	14	1127	139
04-Sep	DFO	DFO_002	43.34	-79.67	63.5	62.9	4 (2)	109	7	729	46
05-Sep	DFO	CSMI_012	43.50	-79.35	109.5	107.5	3 (2)	103	10	463	46
05-Sep	DFO	DFO_009	43.59	-79.39	66	67.25	4	41	18	180	77
06-Sep	DFO	CSMI_019	43.38	-79.29	107.5	105.5	3 (2)	265	33	1465	180
21-Oct	DFO	CSMI_012	43.50	-79.35	108	106	6 (4)	145	39	697	186
21-Oct	DFO	DFO_009	43.59	-79.39	62	60	4	5	0.5	15	1
22-Oct	DFO	CSMI_018	43.30	-79.28	85	83	5	34	8	209	47

Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
22-Oct	DFO	CSMI_019	43.38	-79.29	108	106	4	54	6	238	25
23-Oct	DFO	CSMI_033	43.60	-78.80	139	137	2	220	11	1047	54
23-Oct	DFO	CSMI_034	43.46	-78.76	136	134	2	121	23	745	139
23-Oct	DFO	CSMI_055	43.44	-77.44	194	192	3	126	22	170	29
23-Oct	DFO	CSMI_716	43.60	-77.44	170	168	3 (2)	147	33	928	208
23-Oct	DFO	DFO_0B1	43.38	-78.73	52	50	2	0	0	0	
23-Oct	DFO	DFO_0B2	43.39	-78.72	67.5	65.5	2	0	0	0	
23-Oct	DFO	DFO_0B3	43.40	-78.73	91	89	2	9	0.7	36	3
23-Oct	DFO	DFO_33A	43.55	-78.68	155	153	3	161	19	273	31
23-Oct	DFO	DFO_55A	43.52	-77.43	172	170	3 (2)	226	23	1167	121
24-Oct	DFO	CSMI_028	43.77	-78.85	63	61	4 (3)	54	44	268	220
24-Oct	DFO	CSMI_049	43.77	-77.44	44	42	2	0	0	0	
24-Oct	DFO	DFO_49A	43.64	-77.42	125	123	3	117	13	444	49
24-Oct	DFO	DFO_AN2	43.75	-78.85	80.5	78.5	4	84	14	211	35
29-Oct	DFO	CSMI_039	43.48	-78.00	157.5	155.5	2	71	6	331	26
29-Oct	DFO	CSMI_040	43.59	-78.01	187.5	185.5	2	331	73	1734	382
29-Oct	DFO	DFO_3_2	43.66	-78.02	163	161	2	288	44	1425	217
29-Oct	DFO	DFO_39A	43.44	-78.00	115	113	3 (2)	87	10	527	63
30-Oct	DFO	CSMI_041	43.71	-78.03	130	128	3	151	31	524	107
30-Oct	DFO	CSMI_042	43.84	-78.03	68	66	4	48	9	120	23
04-Apr	EPA	CSMI_041	43.71	-78.03	129	125	2	97	5	171	10
05-Apr	EPA	CSMI_049	43.77	-77.44	49	44.5	2 (1)	73	103	85	120
05-Apr	EPA	CSMI_063	43.73	-77.01	87	83	2	12	0.9	27	2

Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
20-May	EPA	CSMI_042	43.84	-78.03	65.2	60	1	23		39	
21-May	EPA	CSMI_018	43.30	-79.28	88	58.5	1	190		759	
21-May	EPA	CSMI_041	43.71	-78.03	134	74.7	1	134		411	
22-May	EPA	CSMI_019	43.38	-79.29	108	66	1	283		315	
23-May	EPA	CSMI_064	43.53	-76.93	224	200	1	423		437	
23-May	EPA	CSMI_065	43.42	-76.88	151	85.3	1	191		723	
18-Jul	EPA	CSMI_027	43.67	-78.83	112	59	1	104		372	
19-Jul	EPA	CSMI_033	43.60	-78.80	134	63	1	387		734	
19-Jul	EPA	CSMI_034	43.46	-78.76	135	68.3	1	126		382	
19-Jul	EPA	CSMI_042	43.84	-78.03	62	35	1	33		80	
20-Jul	EPA	CSMI_039	43.48	-78.00	153	143	1	200		614	
20-Jul	EPA	CSMI_716	43.60	-77.44	147	72.3	1	102		756	
21-Jul	EPA	CSMI_055	43.44	-77.44	190	88.3	1	590		948	
21-Jul	EPA	CSMI_058	43.37	-77.43	160	150	1	236		344	
21-Jul	EPA	CSMI_715	43.63	-76.97	154	81.3	1	190		399	
22-Jul	EPA	CSMI_064	43.53	-76.93	211	100	1	587		604	
22-Jul	EPA	CSMI_065	43.42	-76.88	153	82.5	1	213		1307	
12-Aug	EPA	CSMI_012	43.50	-79.35	103.4	101	2	41	5	180	20
12-Aug	EPA	CSMI_063	43.73	-77.01	86.8	80	2	36	4	124	13
09-Sep	EPA	CSMI_027	43.67	-78.83	113.7	56	1	166		654	
09-Sep	EPA	CSMI_028	43.77	-78.85	65	41.5	1	38		126	
10-Sep	EPA	CSMI_033	43.60	-78.80	135.9	65	1	269		1382	
10-Sep	EPA	CSMI_034	43.46	-78.76	134	64	1	272		1035	

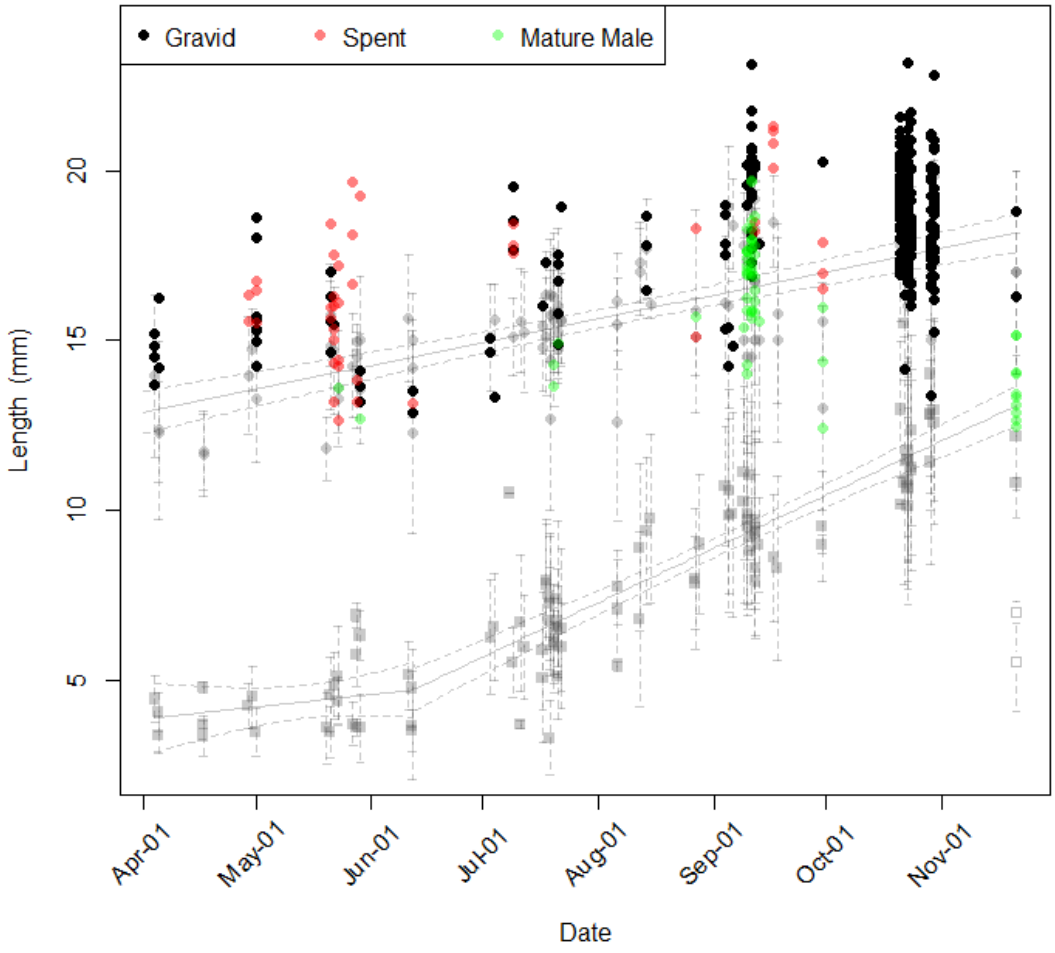
Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
10-Sep	EPA	CSMI_042	43.84	-78.03	66	38.5	1	153		628	
11-Sep	EPA	CSMI_040	43.59	-78.01	182.7	82.3	1	569		1449	
11-Sep	EPA	CSMI_041	43.71	-78.03	131	62.7	1	101		618	
11-Sep	EPA	CSMI_063	43.73	-77.01	87	52	1	62		506	
12-Sep	EPA	CSMI_049	43.77	-77.44	47.6	28.5	1	14		54	
12-Sep	EPA	CSMI_064	43.53	-76.93	213	98.7	1	298		706	
12-Sep	EPA	CSMI_065	43.42	-76.88	144	100	1	74		358	
12-Sep	EPA	CSMI_715	43.63	-76.97	151.2	78.7	1	138		430	
12-Sep	EPA	CSMI_716	43.60	-77.44	147	76.3	1	160		582	
13-Sep	EPA	CSMI_055	43.44	-77.44	188	91	1	216		620	
29-Apr	OMNR	DFO_081	44.02	-76.67	36	34	5	3	2	7	5
30-Apr	OMNR	RP60	43.80	-76.86	60	58	5	7	2	43	12
01-May	OMNR	RP100	43.74	-76.82	100	98	5	37	5	177	25
27-May	OMNR	RP100	43.74	-76.82	100	98	3	48	4	238	22
28-May	OMNR	RP60	43.80	-76.86	60	58	3	3	2	21	13
29-May	OMNR	DFO_081	44.02	-76.67	36	34	3	6	5	16	13
08-Jul	OMNR	DFO_081	44.02	-76.67	36	34	3 (1)	0.7	1.2	2	3
09-Jul	OMNR	RP100	43.74	-76.82	100	98	4	142	17	856	100
17-Jul	OMNR	JulAcs_01	43.72	-76.62	97	90	1	55		300	
17-Jul	OMNR	JulAcs_02	43.65	-76.62	145	100	1	111		476	
18-Jul	OMNR	JulAcs_03	43.44	-78.10	88	90	1	77		484	
19-Jul	OMNR	JulAcs_04	43.76	-78.11	104	100	1	284		891	
20-Jul	OMNR	JulAcs_05	43.43	-78.60	120	100	1	167		462	

Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
21-Jul	OMNR	JulAcs_06	43.70	-78.74	108	100	1	189		418	
16-Sep	OMNR	DFO_081	44.02	-76.67	36	34	3	0	0	0	
17-Sep	OMNR	RP100	43.74	-76.82	100	98	1	125		779	
18-Sep	OMNR	RP20	43.89	-76.86	20	18	3 (1)	0.3	0.6	1	2
18-Sep	OMNR	RP60	43.80	-76.86	60	58	3	16	6	65	24
23-Oct	OMNR	DFO_081	44.02	-76.67	36	34	2	0	0	0	
17-Apr	USGS	OSW2	43.47	-76.67	100	95	1	50		85	
17-Apr	USGS	OSW3	43.45	-76.65	49	49	1	22		79	
17-Apr	USGS	OSW5	43.42	-76.62	6.1	6.1	1	15		2	
28-May	USGS	OSW2	43.47	-76.67	100	100	1	166		868	
28-May	USGS	OSW3	43.45	-76.65	50	50	1	5		12	
28-May	USGS	OSW4	43.43	-76.64	20	20	1	0		0	
28-May	USGS	OSW5	43.42	-76.62	5	5.2	1	0		0	
29-May	USGS	OSW1	43.55	-76.70	200	200	1	397		1073	
12-Jun	USGS	OSW1	43.55	-76.70	200	200	1	376		472	
12-Jun	USGS	OSW2	43.47	-76.67	100	100	1	71		305	
13-Jun	USGS	OSW4	43.43	-76.64	20	20	1	0		0	
13-Jun	USGS	OSW5	43.42	-76.62	5	5	1	0		0	
11-Jul	USGS	OSW2	43.47	-76.67	100	100	1	120		624	
11-Jul	USGS	OSW3	43.45	-76.65	50	50	1	1		0.2	
11-Jul	USGS	OSW4	43.43	-76.64	20	20	1	0		0	
11-Jul	USGS	OSW5	43.42	-76.62	5	5	1	0		0	
12-Jul	USGS	OSW1	43.55	-76.70	200	200	1	283		692	

Date	Crew	Station	Latitude	Longitude	Station Depth	Tow Depth	n	Density	SD	Biomass	SD
06-Aug	USGS	OSW1	43.55	-76.70	196	196	1	942		3678	
06-Aug	USGS	OSW2	43.47	-76.67	98.8	100	1	78		488	
06-Aug	USGS	OSW3	43.45	-76.65	50	48.7	1	13		62	
07-Aug	USGS	OSW4	43.43	-76.64	20	20	1	0		0	
07-Aug	USGS	OSW5	43.42	-76.62	6.3	5	1	0		0	
27-Aug	USGS	OSW1	43.55	-76.70	200	200	1	638		1396	
27-Aug	USGS	OSW2	43.47	-76.67	100	100	1	135		755	
28-Aug	USGS	OSW3	43.45	-76.65	50	50	1	8		16	
28-Aug	USGS	OSW4	43.43	-76.64	20	20	1	0		0	
28-Aug	USGS	OSW5	43.42	-76.62	5	6.7	1	0		0	
30-Sep	USGS	OSW1	43.55	-76.70	200	200	1	441		1357	
30-Sep	USGS	OSW3	43.45	-76.65	50	48	1	13		52	
30-Sep	USGS	OSW5	43.42	-76.62	5	5	1	0		0	
21-Nov	USGS	OSW1	43.55	-76.70	200	200	1	109		506	
21-Nov	USGS	OSW2	43.47	-76.67	100	100	1	5		15	
21-Nov	USGS	OSW3	43.45	-76.65	50	50	1	0		0	
21-Nov	USGS	OSW4	43.43	-76.64	20	20	1	4		6	
21-Nov	USGS	OSW5	43.42	-76.62	5	5.7	1	4		2	

APPENDIX 2

Length of reproductive individuals (gravid and spent females and mature males) plotted against date, and overlaid on plot of mean cohort size +/- 1 SD for Y0 and Y1 cohorts and growth rate regressions ± 2 SE. Individuals were caught in whole-water-column vertical net tows. I include the methods used to determine reproductive status of *M. diluviana* in the *Sample processing* section of Methods for *Chapter 2*. Note that I do not currently have the proportion of males that were mature from October 21-30 prepared for publication, yet mature males likely made up 30-50% of age-1 males in the Fall (see *Life history* section of Results for *Chapter 2*).



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